

# THE INDIAN JOURNAL

## OF

# GENETICS & PLANT BREEDING

### CONTENTS

- Studies on hybrid vigour in wheat .. .. S. M. GANDHI,  
T. UMA MENON,  
P. D. BHARGAVA and  
M. P. BHATNAGAR
- Inheritance of seedling resistance to Race 10 of *Puccinia triticina* Erikss. in *Triticum aestivum* crosses .. P. N. BAHL and  
S. P. KOHLI
- Inheritance of seedling resistance to races 13 and H of *Puccinia glumarum* (Schm.) Erikss. and Henn. in crosses of *Triticum aestivum* .. .. P. N. N. NAMBISAN and  
S. P. KOHLI
- Genetic studies in Barley—III. Linkage relations of some plant characters .. .. K. B. L. JAIN
- Studies on World Genetic Stock of Rice (*Oryza sativa* L.)—II. Awning .. .. B. MISRO,  
R. SEETHARAMAN and  
R. H. RICHHARIA
- Genetics of Photoperiod Response in Rice .. .. S. SAMPATH and  
D. V. SESHU
- Cytogenetical effects of X-rays, thermal neutrons and  $\beta$ -particles on *Oryza sativa* L. .. .. S. V. S. SHASTRY and  
K. RAMAIAH
- "Xenia" in Oleiferous *Brassicaceae* .. .. S. S. RAJAN and  
S. B. P. RAO
- Meiotic abnormalities induced by X-rays in *Arachis hypogaea* .. .. S. H. PATIL and  
K. C. BORA
- Mutation studies in annual chrysanthemum—I. Radiation-induced variation in flower form .. .. H. K. JAIN,  
A. K. BOSE,  
D. SATHPATHY and  
S. C. SUR
- Studies in Interspecific and Intergeneric hybrids of *Saccharum*—II. Staminal sterility in certain  $F_1$  hybrids with *S. spontaneum* as the pistil parent .. P. A. KANDASAMI

SB  
123  
I6

OFFICIAL PUBLICATION OF  
THE INDIAN SOCIETY OF GENETICS & PLANT BREEDING  
NEW DELHI



# The Indian Society of Genetics & Plant Breeding

The Society was founded in January 1941 with the following objects:

1. To advance the cause of Genetics and Plant Breeding in India and to encourage and promote study and research in these subjects.
2. To disseminate knowledge of Genetics and Plant Breeding.
3. To provide facilities for association and conference among students of heredity and for the encouragement of close relationship between workers in Genetics and Plant Breeding and those in the related sciences.

## EXECUTIVE COUNCIL FOR 1961

<i>President:</i>	DR. E. K. JANAKI AMMAL, Jammu
<i>Vice-Presidents:</i>	DR. A. R. GOPAL-AYENGAR, Bombay DR. A. B. JOSHI, New Delhi
<i>Secretary:</i>	DR. M. S. SWAMINATHAN, New Delhi
<i>Treasurer:</i>	DR. M. L. MAGOON, New Delhi
<i>Councillors:</i>	DR. S. M. SIKKA, New Delhi DR. S. GOVINDASWAMI, Cuttack PROF. P. N. BHADURI, Calcutta DR. B. S. KADAM, Poona DR. G. P. ARGIKAR, Poona DR. K. RAMIAH, Bangalore
<i>Editor:</i>	DR. B. P. PAL, New Delhi
<i>Assistant Editor:</i>	MR. S. RAMANUJAM, New Delhi

---

## The Indian Journal of Genetics & Plant Breeding

Edited  
by  
B. P. PAL

THE INDIAN JOURNAL OF GENETICS & PLANT BREEDING, which is the official publication of the Society, will be published three times a year for the present. In 1941 there was only one number, and two numbers were published each year till 1959. The subscription rate (for non-members) is Rs. 20 per year inclusive of postage.

A limited amount of space is available for the insertion of advertisements of interest to geneticists and plant breeders. Communications regarding advertisements and other business matters should be addressed to the Secretary, The Indian Society of Genetics & Plant Breeding, Indian Agricultural Research Institute, New Delhi-12.

# THE INDIAN JOURNAL OF GENETICS AND PLANT BREEDING

Vol. 21, No. 1

## TABLE OF CONTENTS

	Pages
Studies on hybrid vigour in wheat—S. M. Gandhi, T. Uma Menon, P. D. Bhargava and M. P. Bhatnagar .. .. .	1-10
Inheritance of seedling resistance to Race 10 of <i>Puccinia triticina</i> Erikss. in <i>Triticum aestivum</i> crosses —P. N. Bahl and S. P. Kohli .. .. .	11-14
Inheritance of seedling resistance to races 13 and H of <i>Puccinia glumarum</i> (Schm.) Erikss. and Henn. in crosses of <i>Triticum aestivum</i> —P. N. N. Nambisan and S. P. Kohli .. .. .	15-22
Genetic studies in Barley—III. Linkage relations of some plant characters— K. B. L. Jain .. .. .	23-33
Studies on World Genetic Stock of Rice ( <i>Oryza sativa</i> L.)—II. Awning— B. Misro, R. Seetharaman and R. H. Richharia .. .. .	34-37
Genetics of Photoperiod Response in Rice—S. Sampath and D. V. Seshu	38-42
Cytogenetical effects of X-rays, thermal neutrons and $\beta$ -particles on <i>Oryza</i> <i>sativa</i> L.—S. V. S. Shastry and K. Ramaiah .. .. .	43-51
“Xenia” in Oleiferous <i>Brassicae</i> —S. S. Rajan and S. B. P. Rao .. .. .	52-58
Meiotic abnormalities induced by X-rays in <i>Arachis hypogoea</i> —S. H. Patil and K. C. Bora .. .. .	59-67
Mutation studies in annual chrysanthemum—I. Radiation-induced variation in flower form—H. K. Jain, A. K. Bose, D. Sathpathy and S. C. Sur	68-74
Studies in Interspecific and Intergeneric hybrids of <i>Saccharum</i> —II. Staminal sterility in certain $F_1$ hybrids with <i>S. spontaneum</i> as the pistil parent— P. A. Kandasami .. .. .	75-76





# THE INDIAN JOURNAL OF GENETICS & PLANT BREEDING

VOL. 21

MARCH 1961

No. 1

## STUDIES ON HYBRID VIGOUR IN WHEAT

S. M. GANDHI, T. UMA MENON, P. D. BHARGAVA and M. P. BHATNAGAR

*Central Agricultural Research Station, Durgapura (Rajasthan)*

### ERRATA

Volume 18, No. 2, December 1958 (Issued: August, 1959)

Page 116 Line 4                      FOR     B. P. PAL, G. S. MURTY and AMIR SINGH

   READ   B. P. PAL, G. S. MURTY, S. SEN and  
   AMIR SINGH

Volume 19, No. 1, June 1959 (Issued: March, 1960)

Page 36 Line 2                      FOR     B. P. PAL, G. S. MURTY, AMIR SINGH  
   and DALJIT SINGH

   READ   B. P. PAL, G. S. MURTY, S. SEN, AMIR  
   SINGH and DALJIT SINGH

standardisation may be applied in case of wheat, the next important step is to examine the possibility of this crop being suitable for the exploitation of hybrid vigour. Selection of suitable parents, which in addition to good combining ability must also combine the best agronomic features for seed quality, ear characters and straw strength, is an important step.

Pioneering work in this respect has already been contributed by Engledow and Pal (1934) and Pal and Nek Alam (1938). The behaviour of the hybrids in comparison to the parents belonging to a single species of wheat has been studied with respect to grain yield, tillering and germination of the seeds. It is evident from these studies that there does exist some heterosis in wheat crosses. It has also been suggested that wheat exhibits heterosis more clearly than barley (Engledow and Pal, 1934). Recent studies at the I.A.R.I., have also shown that hybrids between some Indian varieties and some exotic South American varieties like Rio Negro, Frontiera and others possess considerable heterotic vigour (Pal and Sikka, 1956).



To further advance such studies, an experiment was taken up by the authors where eleven rust resistant varieties of wheat, exotic and indigenous, were crossed with an improved variety, R.S. 31-1. The latter has been evolved by crossing C. 591 and Jaipur local and enjoys wide suitability in many parts of Rajasthan. Apart from hybrid vigour in respect of different characters, the varieties were also assessed for their combining ability since one of the parents, R.S. 31-1, is common to all the crosses.

#### MATERIALS AND METHODS

The eleven rust-resistant exotic and indigenous parents used in the cross combinations have been utilised in the hybridisation programme in Rajasthan for evolving rust resistant varieties of wheat. Details regarding their rust resistance under Indian conditions and the place of their origin are given below:

Variety	Place of origin	Rust Reaction
E. G. 953	Egypt	Resistant to black and yellow rusts.
E. G. 954	Egypt	Moderately resistant to all the three rusts.
E. G. 1057	Egypt	Resistant to black and moderately resistant to yellow rust.
E. G. 1440	Egypt	Resistant to yellow and brown rusts.
Cometo semi-duro	Argentina	Resistant to yellow rust.
Trigo centeira	S. America	Highly resistant to brown and yellow rusts.
Kendee	Australia	Moderately resistant to black rust.
C. 14112	Kenya	Resistant to black rust.
E. 220	Kenya	Resistant to back rust.
N.P. 790	India	Resistant to black rust.
N.P. 785	India	Resistant to yellow rust.

F<sub>1</sub> seeds of the eleven crosses were sown in the *rabi* of 57-58 in an uniform plot on the Government Agriculture Farm, Durgapura. Each hybrid row was accompanied by one parent on either side. It was not possible to replicate the experiment due to the small number of hybrid seeds available. Observations were recorded on the following characters: 1. Plant height in cm. from ground level to the base of the ear, 2. Mean number of tillers per plant, 3. Mean fodder yield of the plant in gm., 4. Mean maximum length of the leaf blade at the second internode from the top (mean of the five leaves), 5. Mean maximum width of the same leaves in cm., 6. 100 grain weight of each plant in gm., 7. Mean number of spikelets per ear (mean of ten ears in each plant), 8. Mean length of the ear in cm. (mean of ten ears in each plant), 9. Mean grain yield per plant in gm., 10. Days taken from sowing to 75 per cent. flowering.

#### RESULTS

The mean percentage increase or decrease of the eleven hybrids over the mean of the respective parents and over the superior parent with regard to the different characters are given in tables 1 to 4.



*Plant height.*—Except one hybrid, C. 14112  $\times$  R.S. 31-1, all the other hybrids have shown heterotic vigour for height, the  $F_1$ s being superior to the mean of the two parents and also the taller parent. Out of these, seven hybrids were significantly taller than the taller parent (Table 1). The percentage increase varied from 5.78 to 27.27 over the mean of the two parents, while the maximum increase over the superior parent was only 20.54 per cent. In both the cases, the maximum values were obtained in the cross E.G. 1057  $\times$  R.S. 31-1.

*Tillering.*—Extent of heterosis in respect of tillering varied from 5.82 per cent. to 82.35 per cent. in comparison to the mean of the corresponding parents and from 1.58 to 55.55 per cent over the superior parent, the latter value occurring in the hybrid where E. 220, a Kenya variety, was the exotic parent. In five combinations the  $F_1$  hybrids produced a significantly larger number of tillers than the better parent (Table 1). Three out of the eleven crosses, which involved the exotic parents, E.G. 953, C. 14112 and Kendee, have shown negative heterosis when compared to the superior parent. The hybrids, which have shown negative response or very slight increase in plant height over the superior parent, have also exhibited negative heterosis in respect of tillering.

*Fodder yield.*—Five of the hybrid lines involving the exotics E.G. 954, E.G. 1057, Trigo centeira, E. 220 and N.P. 785, are seen to have produced more fodder than the superior parent, the range of variation in vigour being 3.23 to 35.00 per cent. However, only in the cross E. 220  $\times$  R.S. 31-1, is the increase statistically significant (Table 1). The hybrid E. 220  $\times$  R.S. 31-1 has shown the maximum heterotic effect in tillering as well as fodder yield, whereas the hybrid C. 14112  $\times$  R.S. 31-1 has shown the maximum suppression of tillering and fodder yield. This suggests that tillering and fodder yield are closely related. Bhatnagar *et al.*, (1960) have also observed correlation between the yield of straw and the number of tillers in transplanted wheat.

*Leaf length and width.*—The extent of hybrid vigour over the better parent varied from 2.29 to 21.75 per cent. in respect of leaf length and 2.35 to 13.38 per cent. in respect of leaf width. However, the differences were not significant (Table 2). If the first three hybrids in order of merit, which show either increase or decrease over the superior parents for both leaf length and width are considered (Table 5), it is found that the same hybrids show heterosis for both the characters, which indirectly shows the close association of these characters in inheritance.

*100 Grain weight.*—No conspicuous heterosis is observed for this character. Only four hybrids had heavier grains than the superior parent. The range of the increase was between 0.37 to 5.51 per cent. the maximum being shown by the hybrid E.G. 1057  $\times$  R.S. 31-1. The other seven hybrids showed reduction in grain weight ranging from 4.04 to 29.31 per cent. The hybrids, which have shown an increase in grain weight over the better parent, have not given an increased grain yield. This indicates that factors other than the grain weight may be important in obtaining increased grain yield. The same has also been observed by Argikar and Chavan (1957) in their study of sorghum hybrids.

*Spikelets per ear.*—Heterosis has been least effective in the expression of this character, since all the hybrids except two, have shown negative response when compared with the superior parent. Even in the two hybrids, N.P. 790  $\times$  R.S. 31-1 and E.G. 953  $\times$  R.S. 31-1, where there is an increase over the superior parent, it is less than six per cent. Only the former is significantly superior over the better parent.

*Ear length.*—Although all of the hybrids except one indicated positive hybrid vigour over the mean of the corresponding parents, only six of them were somewhat superior to the better parent. Maximum increase of 8.84 per cent. in comparison to the superior parent was exhibited by the hybrid E.G. 954  $\times$  R.S. 31-1, which is statistically significant (Table 3). The maximum depression has occurred in the cross C. 14112  $\times$  R.S. 31-1. In none of the hybrids, has the increase in ear length been



TABLE 1  
Observations regarding height, tillering and fodder yield in parents and hybrids

Variety or hybrid	Plant height in cm.			Tillers per plant			Fodder yield per plant in gm.		
	Mean value	Percentage increase or decrease of $F_1$ over		Mean value	Percentage increase or decrease of $F_1$ over		Mean value	Percentage increase or decrease of $F_1$ over	
		Mean of parents	Superior parent		Mean of parents	Superior parent		Mean of parents	Superior parent
1	2	3	4	5	6	7	8	9	10
1. E.G. 953 ..	88.64	..	..	12.64	..	..	50.82	..	..
2. E.G. 953 × R.S. 31-1 ..	100.53*	9.77	6.35	17.27	5.82	-15.80	85.83	19.48	-7.57
3. E.G. 954 ..	100.83	..	..	15.83	..	..	68.87	..	..
4. E.G. 954 × R.S. 31-1 ..	112.00	14.66	11.09	23.14*	29.19	15.70	96.28	19.23	3.68
5. E.G. 1057 ..	84.56	..	..	21.88	..	..	77.00	..	..
6. E.G. 1057 × R.S. 31-1 ..	113.95*	27.27	20.54	22.41	7.02	6.99	93.16	9.63	3.23
7. E.G. 1440 ..	107.80	..	..	16.80	..	..	60.00	..	..
8. E.G. 1440 × R.S. 31-1 ..	112.79	11.50	4.63	23.15*	25.81	15.52	75.35	1.40	-18.86
9. Cometo semiduro ..	98.63	..	..	22.18	..	..	79.73	..	..
10. Cometo semiduro × R.S. 31-1 ..	102.16*	5.78	3.58	22.53	6.83	1.58	82.05	4.90	-11.64
11. Trigo centeira ..	103.29	..	..	18.50	..	..	67.10	..	..
12. Trigo centeira × R.S. 31-1 ..	121.72*	23.06	17.85	22.48*	16.78	12.40	99.60	24.53	7.26
13. N.P. 790 ..	91.15	..	..	14.10	..	..	22.30	..	..
14. N.P. 790 × R.S. 31-1 ..	108.91*	17.31	15.21	20.91	22.64	4.5	76.28	32.48	-17.85
15. E. 220 ..	105.60	..	..	14.00	..	..	52.33	..	..
16. E. 220 × R.S. 31-1 ..	120.80*	20.74	14.40	31.00*	82.35	55.55	125.40*	72.76	35.00
17. N.P. 785 ..	86.10	..	..	13.40	..	..	60.60	..	..
18. N.P. 785 × R.S. 31-1 ..	100.58	11.37	6.40	21.85*	30.84	9.25	115.83	50.95	24.70
19. C. 14112 ..	101.46	..	..	11.08	..	..	39.35	..	..
20. C. 14112 × R.S. 31-1 ..	80.17	-18.20	-20.99	10.35	-33.40	-48.25	40.17	-39.22	-56.74
21. Kendec ..	96.47	..	..	14.33	..	..	54.00	..	..
22. Kendec × R.S. 31-1 ..	102.05	6.86	5.78	19.80	15.38	1.00	80.27	9.32	-13.56
23. R.S. 31-1 ..	94.53	..	..	20.00	..	..	92.86	..	..

\*These are significantly superior to the better parent.



TABLE 2  
Observations regarding leaf length, leaf breadth and 100 grain weight in parents and hybrids

Variety or hybrid	Leaf length			Leaf breadth			100 grain weight		
	Mean value	Percentage increase or decrease of $F_1$ over		Mean value	Percentage increase or decrease of $F_1$ over		Mean value	Percentage increase or decrease of $F_1$ over	
		Mean of parents	Superior parent		Mean of parents	Superior parent		Mean of parents	Superior parent
1	2	3	4	5	6	7	8	9	10
1. E.G. 953 ..	22.72	2.29	4.43	1.54	5.81	4.46	5.49	3.31	2.37
2. E.G. 953 × R.S. 31-1 ..	25.08			1.64			5.62		
3. E.G. 954 ..	25.21	16.24	14.10	1.67	14.20	10.77	5.17	1.51	4.04
4. E.G. 954 × R.S. 31-1 ..	29.85			1.85			5.22		
5. E.G. 1057 ..	29.59	11.52	5.04	1.50	10.46	7.64	4.85	11.46	5.51
6. E.G. 1057 × R.S. 31-1 ..	31.08			1.69			5.74		
7. E.G. 1440 ..	32.70	6.56	4.09	1.60	6.96	5.62	3.95	16.42	0.37
8. E.G. 1440 × R.S. 31-1 ..	31.86			1.69			5.46		
9. Cometo semiduro ..	30.59	2.01	9.12	1.83	1.76	5.78	4.27	3.63	7.54
10. Cometo semiduro × R.S. 31-1 ..	27.80			1.73			5.03		
11. Trigo canteira ..	25.13	22.39	19.95	1.51	15.59	13.38	3.30	17.16	5.88
12. Trigo canteira × R.S. 31-1 ..	31.38			1.78			5.12		
13. N.P. 790 ..	26.13	21.80	1.67	1.51	8.44	6.37	4.45	1.01	10.10
14. N.P. 790 × R.S. 31-1 ..	31.85			1.67			4.89		
15. E. 220 ..	30.11	9.49	2.29	1.70	6.75	2.35	3.96	0.42	13.97
16. E. 220 × R.S. 31-1 ..	30.80			1.74			4.68		
17. N.P. 785 ..	31.83	13.97	3.80	1.87	5.81	2.67	3.31	12.13	29.31
18. N.P. 785 × R.S. 31-1 ..	33.04			1.82			3.84		
19. C. 14112 ..	25.19	7.48	9.21	1.56	7.05	7.64	4.09	4.41	8.64
20. C. 14112 × R.S. 31-1 ..	23.75			1.45			4.97		
21. Kendee ..	28.30	8.74	12.19	1.46	1.99	5.73	4.36	15.71	4.23
22. Kendee × R.S. 31-1 ..	24.85			1.48			5.67		
23. R.S. 31-1 ..	26.16			1.57			5.35		

TABLE 3  
Observations regarding spikelets per ear, ear length and grain yield in parents and hybrids

Variety or hybrid	Spikelets per ear			Ear length in cm.			Grain yield per plant in gm.		
	Percentage increase or decrease of $F_1$ over			Percentage increase or decrease of $F_1$ over			Percentage increase or decrease of $F_1$ over		
	Mean value	Mean of parents	Higher parent	Mean value	Mean of parents	Higher parent	Mean value	Mean of parents	Higher parent
1	2	3	4	5	6	7	8	9	10
1. E.G. 953	19.18	2.62	1.00	12.03	3.59	—1.90	28.00	31.70	4.80
2. E.G. 953 × R.S. 31-1	20.01	2.62	1.00	11.80	3.59	—1.90	52.30	31.70	4.80
3. E.G. 954	23.00	4.16	—3.09	10.30	11.21	8.84	27.83	65.4	28.84
4. E.G. 954 × R.S. 31-1	22.29	4.16	—3.09	11.70*	11.21	8.84	64.29	65.4	28.84
5. E.G. 1057	22.50	4.02	—2.22	12.90	9.98	0.77	34.13	40.85	18.20
6. E.G. 1057 × R.S. 31-1	22.00	4.02	—2.22	13.00	9.98	0.77	59.17	40.85	18.20
7. E.G. 1440	25.20	—3.91	—14.21	12.36	4.42	—2.48	30.10	68.71	35.27
8. E.G. 1440 × R.S. 31-1	21.62	—3.91	—14.21	12.06	4.42	—2.48	67.50	68.71	35.27
9. Cometo semiduro	21.10	0.68	—2.42	11.60	4.84	0.95	41.54	21.05	10.86
10. Cometo semiduro × R.S. 31-1	20.59	0.68	—2.42	11.71	4.84	0.95	55.32	21.05	10.86
11. Trigo centeira	24.00	5.94	—3.45	11.99	9.40	3.75	13.30	69.00	7.02
12. Trigo centeira × R.S. 31-1	23.20	5.94	—3.45	12.44	9.40	3.75	53.40	69.00	7.02
13. N.P. 790	20.00	6.43	5.90	12.12	12.60	6.18	16.30	12.60	—25.31
14. N.P. 790 × R.S. 31-1	21.18*	6.43	5.90	12.87	12.60	6.18	37.27	12.60	—25.31
15. E. 220	22.33	1.61	—4.17	13.43	8.52	—2.31	13.33	80.95	14.63
16. E. 220 × R.S. 31-1	21.40	1.61	—4.17	13.12	8.52	—2.31	57.20	80.95	14.63
17. N.P. 785	25.60	—4.98	—15.77	8.92	2.03	—6.69	13.60	35.43	—13.82
18. N.P. 785 × R.S. 31-1	21.57	—4.98	—15.77	10.03	2.03	—6.69	43.00	35.43	—13.82
19. C. 14112	18.86	—21.02	—23.79	10.81	—14.75	—14.98	19.36	—27.08	—49.40
20. C. 14112 × R.S. 31-1	15.09	—21.02	—23.79	9.19	—14.75	—14.98	25.25	—27.08	—49.40
21. Kendee	19.44	—5.96	—6.82	9.68	6.26	0.93	21.22	37.04	—2.35
22. Kendee × R.S. 31-1	18.45	—5.96	—6.82	10.85	6.26	0.93	48.73	37.04	—2.35
23. R.S. 31-1 (Common parent)	19.80	..	..	10.75	..	..	49.90	..	..

\*These are significantly superior to the better parent.



followed by an increase in the number of spikelets per ear, except in N.P. 790  $\times$  R.S. 31-1 where there is an increase of about six per cent. in both the characters.

*Grain yield.*—Since the common parent in the present study is an improved local variety in Rajasthan, this has given the highest grain yield over all the rust resistant parents used in the crosses and as such is the superior parent for all the cross combinations. Ten out of the eleven hybrids are better than the mean of the corresponding parents while seven hybrids have yielded 4.8 to 35.3 per cent. more than the superior parent though none were significantly superior to it.

*Days to 75 per cent. flowering.*—All the ten hybrids observed have shown earlier ear-emergence than the corresponding late parent, the maximum being noticed in the hybrids, Kendee  $\times$  R.S. 31-1 and E.G. 1440  $\times$  R.S. 31-1. All the exotic parents used in the crosses were late in comparison to the common parent, R.S. 31-1, which flowered in 78 days. The range in days taken by the rust resistant parents for 75 per cent. flowering varied from 87 to 110 days. None of the hybrids eared earlier than the earliest parent, while five of the hybrids have eared in about the same number of days as the earliest parent, R.S. 31-1, showing the clear dominance of earliness in these crosses.

TABLE 4

*Observation regarding days taken for 75 per cent. flowering in parents and hybrids*

Parent or hybrid	Mean value	Percentage increase or decrease of $F_1$ over	
		Mean of parents	Superior parent
1. E.G. 953 .. ..	90		
2. E.G. 953 $\times$ R.S. 31-1 .. ..	85	+1.19	-5.55
3. E.G. 954 .. ..	99		
4. E.G. 954 $\times$ R.S. 31-1 .. ..	87	-2.25	-12.13
5. E.G. 1057 .. ..	91		
6. E.G. 1057 $\times$ R.S. 31-1 .. ..	87	+4.82	-4.40
7. E.G. 1440 .. ..	105		
8. E.G. 1440 $\times$ R.S. 31-1 .. ..	84	-8.70	-20.00
9. Cometo semiduro .. ..	89		
10. Cometo semiduro $\times$ R.S. 31-1 .. ..	79	-5.95	-11.24
11. Trigo centeira .. ..	110		
12. Trigo centeira $\times$ R.S. 31-1 .. ..	88	-6.38	-10.91
13. N.P. 790 .. ..	87		
14. N.P. 790 $\times$ R.S. 31-1 .. ..	80	-3.61	-8.04
15. E. 220 .. ..	91		
16. E. 220 $\times$ R.S. 31-1 .. ..	78	-8.23	-14.29
17. N.P. 785 .. ..	..	..	..
18. N.P. 785 $\times$ R.S. 31-1 .. ..	..	..	..
19. C. 14112 .. ..	95		
20. C. 14112 $\times$ R.S. 31-1 .. ..	78	-10.35	-17.89
21. Kendee .. ..	101		
22. Kendee $\times$ R.S. 31-1 .. ..	80	-11.11	-20.79
23. R.S. 31-1 .. ..	78	..	..

*Combining ability.*—R.S. 31-1, a local improved variety of the place, has been used as common parent in the crosses studied in the present investigation and as such a good idea about the combining ability of the rust resistant parents with the common variety can be obtained. The hybrids with four Egyptian wheat exotics viz. E.G. 953, E.G. 954, E.G. 1057 and E.G. 1440, with Cometo semiduro and Trigo centeira from Latin America and with E. 220 from Kenya, have given higher grain yields than the superior parent. The variety E.G. 1440 appears to possess the best combining ability for grain yield, since the hybrid resulting from its cross has recorded the highest grain yield.

TABLE 5

*Details about the hybrids giving the highest and the lowest values over the superior parent*

Characters	Hybrid or Hybrids			
	Showing highest value over the superior parent	First three in order of merit showing the highest value over the superior parent	Showing lowest value over the superior parent	First three in order of merit showing the lowest value over the superior parent
1. Plant height ..	6*	6, 12, 14	20	..
2. Tillers ..	16	16, 4, 8	20	20, 2, 22
3. Fodder yield ..	16	16, 18, 12	20	20, 8, 14
4. Leaf length ..	14	14, 12, 4	22	22, 20, 10
5. Leaf width ..	12	12, 4, 6	20	20, 10, 22
6. 100 grain weight ..	6	6, 22, 2	18	18, 16, 20
7. Spikelets per ear ..	14	14, 2	20	20, 18, 8
8. Ear length ..	4	4, 14, 12	20	20, 18, 8
9. Grain yield ..	8	8, 4, 6	20	20, 14, 18
10. Days to flower ..	..	..	22†	22, 8, 20

\*Numbers relate to hybrids in Tables 1, 2, 3 and 4. †Over the late parents.

As regards fodder yield, only five hybrids involving the exotics E. 220, N.P. 785, E.G. 954, E.G. 1057 and Trigo centeira, have given higher fodder yields over the best parent, the last three giving only a marginal increase of about 3 to 7 per cent. The Kenya variety E. 220, is the best combiner for fodder yield, since the hybrid involving this variety has given 35 per cent. increased yield over the superior parent and 72.76 per cent. over the mean of the parents.

Exotic E.G. 1440 which is the best combiner for grain yield, has shown very poor combination for fodder yield. Another interesting observation is that exotic C. 14112 from Kenya has shown a depressing effect on all the characters studied and in most of the cases the reduction over the superior parent is the highest (Table 5).

#### DISCUSSION

Although exploitation of heterosis in wheat is still beset with many practical difficulties for want of easy methods of emasculating and pollinating, the economic



importance of the crop and the pivotal role it plays in the dietary of the nation, makes it highly desirable that all possible attempts should be made to exploit hybrid vigour in this crop also. The present investigation, which records the hybrid vigour present in eleven wheat crosses, is one of the steps in this direction.

Except in the characters, spikelets per ear, ear length and 100 grain weight, considerable heterosis is evident in all the other features like height, tillering, leaf length, leaf width, grain yield and fodder yield. For different characters different exotics have given the maximum increase in vigour over the superior parent, when crossed with the common parent. In grain yield per plant, seven hybrids have yielded more than the superior parent, R.S. 31-1, the increase ranging from 4.80 to 35.27 per cent. The highest yield has been observed where E.G. 1440 was the exotic parent. The next best exotic is another Egyptian variety E.G. 954, which has been responsible for giving about 29 per cent greater yield than R.S. 31-1. It is significant to note that none of the hybrids have yielded less than the respective inferior parent and only one, C. 14112  $\times$  R.S. 31-1, has proved inferior to the mean of the corresponding two parents.

Among the components of grain yield, which have been considered in the present study, number of tillers seems to exert the maximum influence in obtaining increased grain yield in the hybrids. Only in the hybrid E. 220  $\times$  R.S. 31-1 is some reduction noticed but in this instance substantial decrease in 100 grain weight seems to be more responsible for decreasing the ultimate grain yield. The other yield components like spikelets per ear, ear length and 100 grain weight contribute the least to the higher grain yield of the hybrids in the present study.

In respect of fodder yield only two of the hybrids—E. 220  $\times$  R.S. 31-1 and N.P. 785  $\times$  R.S. 31-1, have been able to manifest high heterotic vigour ranging from about 25 to 35 per cent. over the superior parent, but these two hybrids have actually been poor in their grain yield. Among the components of fodder yield like plant height, tillers, leaf length and leaf width, only increased tillers per plant appear to contribute towards the increase in fodder yield of the hybrids.

In one hybrid, C. 14112  $\times$  R.S. 31-1, all the characters including the grain and fodder yield, have shown suppression and in seven out of the ten characters, reduction from the superior parent is maximum in this cross (Table 5).

Although hybrid vigour upto a maximum of about 36 per cent. in grain yield has been obtained in the present investigation and seven of the hybrids have out-yielded the superior parent, R.S. 31-1, further research is needed to explore a wider range of material with better genic combinations so that higher heterotic vigour may be obtained as has been noticed in the cross—pollinated crops like maize.

#### SUMMARY

Eleven rust resistant wheat varieties, exotic and indigenous, were crossed with a common parent, R.S. 31-1, an improved high yielding but rust susceptible local variety, for studying the hybrid vigour and the combining ability of the rust resistant parents. Observations were recorded for a number of characters like plant height, tillering, leaf length and leaf width, spikelets per ear, ear length, 100 grain weight, 75 per cent. flowering, fodder yield and grain yield.

Heterosis is evident in all the characters except ear length, spikelets per ear and 100 grain weight. It is observed that hybrids gave increases in yield of grain from 4.80 per cent. to as high as 35.27 per cent. and for fodder yield from 3.23 to 35.00 per cent. Highest value for heterosis has been observed in tillering where the hybrid E. 220  $\times$  R.S. 31-1 showed an increase of about 56 per cent. over the superior parent.

The variety E.G. 1440 from Egypt has shown the best combining ability with R.S. 31-1 for grain yield whereas a black-rust resistant variety from Kenya, E. 220,

has shown the best combining ability in respect of fodder yield. Another variety from Kenya, C. 14112, has shown a depressing effect on all the characters studied and in seven of the characters the decrease over the superior parent is maximum in the cross involving this variety.

#### ACKNOWLEDGEMENTS

The authors wish to express their gratefulness to Shri Samarth Raj, Director of Agriculture and Food Commissioner, for providing necessary facilities to carry out this work.

#### REFERENCES

- Argikar, G. P. and Chavan, V. M. (1957). A study of heterosis in *Sorghum*. *Indian J. Genet.*, **17**: 65-72.
- Bhatnagar, M. P., Bhargava, P. D. and Gandhi, S. M. (1960). Effect of transplanting on wheat. *J. Indian bot. Soc.*, (In press).
- Engledow, F. L. and Pal, B. P. (1934). Investigation on yield in cereals. VIII. Hybrid vigour in wheat. *J. agric. Sci.*, **24**: 390.
- Joshi, B. S., Singh, H. B. and Gupta, P. S. (1958). Studies in hybrid vigour. III. *Bhindi*. *Indian J. Genet.*, **18**: 57-68.
- Pal, B. P. (1945). Studies in hybrid vigour. I. Notes on the manifestation of hybrid vigour in gram, sesamum, chilli and maize. *Indian J. Genet.*, **5**: 106-21.
- and Nek Alam (1938). The effect of certain external factors upon the manifestation of hybrid vigour in wheat. *Proc. Indian Acad. Sci.*, **7B**: 109.
- and Singh, H. B. (1946). Studies in hybrid vigour. II. Notes on the manifestation of hybrid vigour in the brinjal and bitter gourd. *Indian J. Genet.*, **6**: 19-33.
- and Sikka, S. M. (1956). Exploitation of hybrid vigour in the improvement of crop plants, fruits and vegetables. *Indian J. Genet.*, **16**: 98-104.
- Sikka, S. M. and Swaminathan, M. S. (1956). Cytogenetics in relation to wheat improvement. *Paper presented at the Wheat Research Workers' Conference, Simla*.
- Wittwer, S. H. and Hillyer, J. C. (1954). Chemical induction of male sterility in cucurbits. *Science*, **120**: 893.



# INHERITANCE OF SEEDLING RESISTANCE TO RACE 10 OF *PUCCINIA TRITICINA* ERIKSS. IN *TRITICUM AESTIVUM* CROSSES

P. N. BAHL and S. P. KOHLI

*Wheat Breeding Substation, I.A.R.I., Simla*

RUSTS are the most serious of all the fungal diseases that attack the wheat crop in India. Of the three rusts of wheat, black and brown cause greatest damage to the crop in the important wheat growing states. The latter is particularly severe under mild temperature conditions of the North Indian plains and low elevation hills. Of the prevalent races of brown rust in the country, *viz.*, 10, 11, 17, 20, 26, 63, 70, 77, 106, 107, 108 and 162, races 10, 20 and 63 are the most frequently encountered, (Mehta, 1933; Vasudeva *et al.*, 1955). Under the hybridization programmes for incorporating rust resistance, N.P. 770 and N.P. 809 were crossed with a number of foreign donors of resistance. The available hybrid material was utilized for the study of the mode of inheritance of resistance to race 10.

Though great strides have been made in the matter of breeding high yielding and superior quality wheats in India, the work for systematic breeding for resistance to rusts had been taken up somewhat later when the information regarding the prevalent race flora had been gathered. Very little is known regarding the mode of inheritance of resistance to brown rust races met with in this country. Of the large number of exotics tested for resistance to the brown rust races prevalent in India, Frontiera, Frondoso, and La Prevision among others have been found to be resistant and have been extensively used in the hybridization programmes under way for breeding for brown-rust resistance.

## MATERIALS AND METHODS

As stated earlier, race 10 of *P. triticina* is quite widespread in its distribution in India. It was, therefore, considered desirable to study the mode of inheritance of resistance to this race, obtained from the two sources, *viz.*, Frontiera (E. 957) and La Prevision (E. 928) in crosses with N.P. 770 and N.P. 809 respectively.

The studies were conducted during February to April, 1958 in the spore-proof glass-house at the Wheat Breeding Substation, Simla. A susceptible variety, Agra Local, as well as the parental varieties were inoculated along with the crosses so as to enable comparison of their reactions with those of the hybrid seedling. Classification of plants was done according to the system proposed by Mains and Jackson (1926) and later modified by Johnston and Mains (1932). Resistant (0, 1 and 2), semi-resistant (2-3) and susceptible (3 and 4) classes were recognised. The individual plants of each set of material were re-observed for their rust reaction a few days after making the first observation. Brief description of the parents entering the two cross combinations studied are given below:

*Frontiera* (E. 957) is a South American wheat that has been found to be resistant to the Indian races of brown rust *viz.*, 10, 11, 17, 20, 26, 63, 70, 106, 107 and 108 and susceptible only to races 77 and 162. The seedling reaction of Frontiera to race 10 was of types 0 and 0.

*La Prevision* (E. 928) too is a South American variety that has been tested against brown rust races 10, 11, 20, 26, 63, 106, 107 and 108 and found to be resistant to all of them. The variety showed 0 and 0; types of seedling reactions against race 10.

The seedling stage reaction of N.P. 770 against race 10 was of the types 3 and 4.

N.P. 809 gave 3 and 4 types of seedling reactions when tested against race 10 of brown rust.

The parents,  $F_1$ ,  $F_2$  and  $F_3$  generations of two crosses *viz.*, (N.P. 770  $\times$  E. 957) and (La Prevision  $\times$  N.P. 809) were studied during 1958, under optimum conditions for rust development. The number of seedlings tested in each of the  $F_3$  generation families varied from about 11-15. Since the number of seedlings tested in each of the individual  $F_3$  family was small, no genetic ratios were fitted to the data from the  $F_3$  lines.

#### EXPERIMENTAL RESULTS

##### (i) Resistance of Frontiera to Race 10 of *P. triticina*:

The parental,  $F_1$ ,  $F_2$  and  $F_3$  seedling reaction data of the cross N.P. 770  $\times$  Frontiera as also the expected frequencies of  $F_2$  population under different classes are summarised in table 1.

TABLE 1

Seedling reaction of the parents,  $F_1$ ,  $F_2$  generations and  $F_3$  progenies of the cross, N.P. 770  $\times$  Frontiera, tested against race 10 of *P. triticina*.

Material tested	Reaction to race 10			Total	$X^2$	P value
	Resistant	Segre- gating	Suscep- tible			
N.P. 770 .. ..	..	..	17	..	..	..
Frontiera .. ..	18	..	..	..	..	..
(N.P. 770 $\times$ Frontiera) $F_1$	1	..	8	9	..	..
(N.P. 770 $\times$ Frontiera) $F_2$	..	..	..	..	..	..
(Observed)	4	..	255	259	..	..
(N.P. 770 $\times$ Frontiera) $F_2$	..	..	..	..	..	..
(expected on 1R:63S basis)	4.04	..	254.96	259	0.001	0.99 to 0.98
(N.P. 770 $\times$ Frontiera) $F_3$	..	..	..	..	..	..
families (Observed)	3	43	54	100	..	..
(N.P. 770 $\times$ Frontiera) $F_3$	..	..	..	..	..	..
families (expected on 1R:26Seg:37S)	1.56	40.63	58.81	100	1.860	0.50 to 0.30

It will be observed from the data summarised in the above table that the resistance of Frontiera was recessive in the  $F_1$  generation. The one resistant  $F_1$  plant had probably escaped infection. In the  $F_2$  generation, a three factor ratio of 1R:63S was obtained. Of the 100  $F_3$  families tested, only three were seen to be homozygously resistant, 43 segregated into resistant and susceptible plants while 54 bred pure for susceptibility, thus giving the expected ratio of 1R:26Seg:37S.

##### (ii) Resistance of La Prevision to race 10 of *P. triticina*:

The resistance of La Prevision to race 10 of leaf rust was studied in the cross, La Prevision  $\times$  N.P. 809. The parental,  $F_1$ ,  $F_2$  as well as the  $F_3$  families' reaction to this race are summarised in table 2.



TABLE 2

*Seedling reactions of the parental,  $F_1$ ,  $F_2$  populations and  $F_3$  progenies of the cross La Prevision  $\times$  N.P. 809, against race 10 of *P. triticea**

Material tested	Reaction to race 10			Total	$X^2$	P value
	Resistant	Segre- gating	Suscep- tible			
La Prevision ..	20	..	..	20	..	..
N.P. 809 ..	..	..	22	22	..	..
(La Prevision $\times$ N.P. 809) $F_1$ ..	..	..	8	8	..	..
(La Prevision $\times$ N.P. 809) $F_2$ (Observed) ..	2	..	290	292	..	..
(La Prevision $\times$ N.P. 809) $F_2$ (expected on 1R:63S basis) ..	4.56	..	287.44	292	1.458	0.30 to 0.20
(La Prevision $\times$ N.P. 809) $F_3$ (Observed) ..	2	32	40	74	..	..
(La Prevision $\times$ N.P. 809) $F_3$ (expected on 1R: 26Seg: 37S basis) ..	1.16	30.06	42.78	74	0.914	0.70 to 0.50

Susceptibility of N.P. 809 was seen to be dominant over the resistance of La Prevision. The  $F_2$  generation segregation gave evidence of a tri-hybrid ratio of 1R: 63S. This was later confirmed by the behaviour of the  $F_3$  progenies.

#### DISCUSSION

The experimental results reported in this paper show that the resistance of Frontiera and La Prevision to race 10 of brown rust have behaved alike. The  $F_2$  data suggested the operation of three genes conditioning the rust reaction in these two cases.

Cases of resistance to brown rust races being governed by a single (Waterhouse, 1930) or two pairs (Schmidt *et al.*, 1953) of genes have also been reported. The studies of Martinez, Ausemus and Burnham (1953) showed that the adult plant resistance of NS No. II-39-2 was due to three genes. Mains *et al.* (1926), however, found the seedling as well as the adult plant resistance of Kanred and Malkoff to a mixture of races of leaf rust to be due to the action of a number of genes. The available evidence, therefore, shows that the resistance of varieties to leaf rust may be due to one or more genes.

Using a mixture of all the Indian races of brown rust in the inheritance studies conducted by Ghosh *et al.* (1958), the adult plant resistance of Frontiera in its cross with Ph.C. 591, was seen to be recessive and conditioned by a single pair of genes. Pal *et al.* (1956) found the resistance of Frondoso against the Indian brown rust races in the adult plant stage to be governed by two pairs of dominant complementary genes.

## SUMMARY

The resistance of the two South American wheats, *viz.*, Frontiera and La Prevision to race 10 of *P. triticina* in the crosses, *viz.* N.P. 770  $\times$  Frontiera and La Prevision  $\times$  N.P. 809 was seen to be controlled by three genes—all of which when present together in a recessive condition result in resistance.

## ACKNOWLEDGEMENTS

The authors wish to thank the Head of the Division of Mycology and Plant Pathology, Indian Agricultural Research Institute, New Delhi and his staff at Simla for kindly supplying the initial inoculum. The interest evinced by Dr. B. P. Pal, Director, I.A.R.I., New Delhi in these studies enabled the successful completion of this work.

## REFERENCES

- Ghosh, Suva, Sikka, S. M. and Rao, M. V. (1958). Inheritance studies in Wheat IV—Inheritance of Rust Resistance and other characters. *Indian J. Genet.*, **18**: 142-62.
- Johnston, C. O. and Mains, E. B. (1932). Studies on physiologic specialization in *Puccinia triticina*. *Tech. Bull. U.S. Dept. Agric.*: 313.
- Mains, E. B. and Jackson, H. S. (1926). Physiological specialization in the leaf rust of wheat, *Puccinia triticina* Erikss. *Phytopathology*, **16**: 89-120.
- Martinez, M. L., Ausemus, E. R. and Burnham, C. R. (1953). Inheritance of reaction to leaf rust, *Puccinia rubigo-vera tritici* (Erikss.) Carl., and of certain other characters in a wheat cross. *Tech. Bull. Minn. agric. Exp. Sta.*: 205.
- Mehta, K. C. (1953). Rusts of wheat and barley in India. *Ind. J. agric. Sci.*, **3**: 939-62.
- Pal, B. P., Sikka, S. M. and Rao, M. V. (1956). Inheritance studies in wheat. *Indian J. Genet.*, **16**: 32-46.
- Schmidt, J. W., Hayne, E. G., McCreacken, E., Johnston, C. O. and Hasket, W. C. (1953). Wheat Genetic and Cytogenetic research at Kansas State College. *Rept. Intern. Wheat Stem Rust Conf., Winnipeg, Canada*. 96-97 (original not seen).
- Vasudeva, R. S., Prasada, R., Lele, V. C., Joshi, L. M. and Kak, D. (1955). Prevalence of physiologic races of wheat and barley rusts in India. *Indian Phytopath.*, **8**: 22-51.
- Waterhouse, W. L. (1930). Australian rust studies, III. Initial results of breeding for rust resistance. *Proc. Linn. Soc., N.S.W.*, **55**: 596-636.



# INHERITANCE OF SEEDLING RESISTANCE TO RACES 13 AND H OF *PUCCINIA GLUMARUM* (SCHM.) ERIKSS. AND HENN. IN CROSSES OF *TRITICUM AESTIVUM*

P. N. N. NAMBIAN and S. P. KOHLI

*Wheat Breeding Substation, I.A.R.I., Simla*

OF the three rusts attacking the wheat crop in India, yellow rust, *Puccinia glumarum* (Schm.) Erikss. and Henn., is wide-spread in its distribution and may become quite a devastating disease in the hills, where the prevailing low temperature conditions favour its assuming epidemic proportions rather frequently. In some areas, it is the limiting factor in the successful cultivation of wheat and barley crops. Though marked success has been achieved in breeding wheat varieties resistant to yellow rust, particularly for the hills, little information is available on the genetics of resistance to this rust. An attempt was, therefore, made to study the resistance to races 13 and H of this rust in varietal crosses of *Triticum aestivum*. Both the races are frequently picked up from the different wheat growing areas of India and race 13 is becoming more wide-spread during the recent years.

## MATERIALS AND METHODS

A number of exotic varieties have been utilized in the breeding programmes at the Indian Agricultural Research Institute and its substation at Simla for the breeding of rust resistant wheats in the country. Of these, the following have entered the cross combinations with hill-wheats and were available for seedling inheritance studies:

- |                         |   |
|-------------------------|---|
| Cometa Klein (E. 671):  | The variety is resistant to almost all the Indian races of yellow rust including H and 13.  |
| Frondoso (E. 771) :     | The variety is resistant to most of the Indian races of brown and yellow rusts.   |
| La Prevision (E. 928) : | The variety possesses resistance to yellow rust races 13 and H as also to most of the Indian races of black rust.   |
| Frontiera (E. 957) :    | The variety is resistant to almost all the Indian races of brown rust and race H of yellow rust.  |
| Ridley (E. 572) :       | An introduction from Australia. It is susceptible to yellow rust races 13, H and a few others.  |
| N.P. 770 :              | Though highly resistant to yellow rust in the adult-plant stage, this variety is, however, susceptible to all the races of this rust in the seedling stage. |

The seedling resistance tests reported in this study were conducted in the spore-proof glass house at the Wheat Breeding Substation, Simla, using the usual standard inoculation techniques. The purity of the races was checked by testing their reactions on the international rust 'differentials'. Parents, F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations were tested side by side in order to permit of the comparison of types of reactions of parents and hybrid progenies. 10-14 seedlings grown in four-inch pots were inoculated in the primary-leaf stage. The rust reactions of the seedlings were recorded, when maximum infection had appeared, according to the method adopted by Gassner and Straib

(1930). During cold weather, the pustules took about three weeks to reach their full size.

## RESULTS

### I. Inheritance of resistance to race 13:

The inheritance of resistance to race 13 was studied in four cross combinations, the results of which are reported below:

(i) *Ridley* (E. 572)  $\times$  *La Prevision* (E. 928).—The reaction of the two parents,  $F_1$ ,  $F_2$  and  $F_3$  generations of the cross are given in table 1. Resistance was dominant and the  $F_2$  segregated in a 3R:1S ratio suggesting the existence of one dominant factor for resistance. This was confirmed by the  $F_3$  results.

TABLE 1

*Seedling reaction of the parents,  $F_1$  and  $F_2$  and  $F_3$  of the cross, Ridley  $\times$  La Prevision to race 13*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segregating	Susceptible			
Ridley .. ..	..	..	27	..	..	..
La Prevision ..	20	..	..	..	..	..
(Ridley $\times$ La Prevision) $F_1$	10	..	..	..	..	..
(Ridley $\times$ La Prevision) $F_2$	..	..	..	..	..	..
(observed) ..	217	..	66	283	..	..
(Ridley $\times$ La Prevision) $F_2$	..	..	..	..	..	..
(expected on 3R:1S basis) ..	212.25	..	70.75	283	0.425	0.70 to 0.50
(Ridley $\times$ La Prevision) $F_3$	..	..	..	..	..	..
(Observed) ..	23	44	26	93	..	..
(Ridley $\times$ La Prevision) $F_3$	..	..	..	..	..	..
(expected on 1R:2Seg:1S basis) ..	23.25	40.50	23.26	93	0.460	0.80 to 0.70

(ii) *Frondoso* (E. 771)  $\times$  *N.P. 770*. The reactions of the parents,  $F_1$ ,  $F_2$ ,  $F_3$  of the cross, *Frondoso*  $\times$  *N.P. 770*, are summarised in table 2.

The susceptibility of *N.P. 770* to race 13 was dominant as shown by the behaviour of the  $F_1$  plants. The  $F_2$  and  $F_3$  segregations indicated that a single gene locus was involved.

(iii) *Cometa Klein* (E. 671)  $\times$  *N.P. 770*.—The seedling-resistance data are summarised in table 3.

Unlike in the previous cross, the susceptibility of *N.P. 770* was recessive to the resistance of *Cometa Klein*. The  $F_2$  segregation suggested that two dominant complementary factors might be responsible for the resistance of the exotic variety, *Cometa Klein*. The somewhat unsatisfactory fit in the  $F_3$  is probably due to the rather high temperatures prevailing in the glass house at the time these tests were conducted. This may have prevented the proper development of infection, thereby lowering the proportion of the families grouped in the susceptible class.



TABLE 2

*Seedling reaction of the parents,  $F_1$ ,  $F_2$ , and  $F_3$  of the cross, N.P. 770  $\times$  Frondoso tested against race 13*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segre- gating	Sus- ceptible			
N.P. 770 .. ..	..	..	25	..	..	..
Frondoso .. ..	21	..	..	..	..	..
(N.P. 770 $\times$ Frondoso) $F_1$ ..	..	..	13	..	..	..
(N.P. 770 $\times$ Frondoso) $F_2$ ..	89	..	242	331	..	..
(Observed) .. ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frondoso) $F_2$ ..	82.75	..	248.25	331	0.629	0.50 to 0.30
(expected on 1R:3S basis) .. ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frondoso) $F_3$ ..	20	52	22	94	..	..
(Observed) .. ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frondoso) $F_3$ ..	23.5	47	23.5	94	1.063	0.70 to 0.50
(expected on 1R:2Seg:1S basis) ..	..	..	..	..	..	..

TABLE 3

*Seedling reaction of the parents,  $F_1$ ,  $F_2$  and  $F_3$  of the cross, N.P. 770  $\times$  Cometa Klein, tested against race 13*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segre- gating	Sus- ceptible			
N.P. 770 .. ..	..	..	20	..	..	..
Cometa Klein .. ..	34	..	..	..	..	..
(Cometa Klein $\times$ N.P. 770) $F_1$ ..	12	..	..	..	..	..
(Cometa Klein $\times$ N.P. 770) $F_2$ (Observed) ..	99	..	77	176	..	..
(Cometa Klein $\times$ N.P. 770) $F_2$ (expected on 9R:7S basis) ..	99	..	77	176	No deviation	
(Cometa Klein $\times$ N.P. 770) $F_3$ (Observed) ..	7	50	23	80	..	..
(Cometa Klein $\times$ N.P. 770) $F_3$ (expected on 1R:8Seg:7S basis) ..	5	40	35	80	7.4	0.05 to 0.02

*N.P. 770* × *La Prevision* (E. 928):

The  $F_1$ ,  $F_2$ ,  $F_3$  and parental reactions are summarised in table 4.

TABLE 4

*Seedling reaction of the parents,  $F_1$ ,  $F_2$  and  $F_3$  of the cross, *N.P. 770* × *La Prevision*, tested against race 13*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segregating	Susceptible			
<i>N.P. 770</i> .. .. .	..	..	20	..	..	..
<i>La Prevision</i> ..	22	..	..	..	..	..
( <i>La Prevision</i> × <i>N.P. 770</i> )						
$F_1$ .. .. .	..	..	9	..	..	..
( <i>La Prevision</i> × <i>N.P. 770</i> )						
$F_2$ (Observed) ..	112	..	499	611	..	..
( <i>La Prevision</i> × <i>N.P. 770</i> )						
$F_2$ (expected on 3R : 13S basis) ..	114.6	..	496.4	611	0.071	0.80 to 0.70
( <i>La Prevision</i> × <i>N.P. 770</i> )						
$F_3$ (Observed) ..	4	46	35	85	..	..
( <i>La Prevision</i> × <i>N.P. 770</i> )						
$F_3$ (expected on 1R : 2Seg : 7S basis) ..	5.3	42.6	37.1	85	0.709	0.70 to 0.50

The resistance of *La Prevision* was seen to be due to a pair of dominant genes, the expression of which was suppressed by a dominant pair of genes contributed by the susceptible parent *viz.*, *N.P. 770*.

## II. Inheritance of resistance against Race H:

The resistance of *Frontiera* (E. 957) and *Cometa Klein* (E. 671) to race H of *P. glumarum* was available for study in crosses with *N.P. 770*. The results of these studies are reported below:

(i) *Frontiera* (E. 957) × *N.P. 770*.—The parental,  $F_1$ ,  $F_2$ ,  $F_3$  reactions of the cross (*Frontiera* × *N.P. 770*) are summarised in table 5.

The resistance of *Frontiera* was seen to be due to two pairs of recessive genes contributed by this parent in this cross. The duplicate-factor ratio observed in the  $F_2$  generation was confirmed by the segregation of  $F_3$  lines.

(ii) *Cometa Klein* (E. 671) × *N.P. 770*.—The data regarding the reaction noted in the cross, *Cometa Klein* with *N.P. 770* tested against race H of *P. glumarum* are summarised in table 6.



TABLE 5

*Seedling reaction of the parents,  $F_1$ ,  $F_2$  and  $F_3$  of the cross, N.P. 770  $\times$  Frontiera tested against race H*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segre- gating	Sus- ceptible			
N.P. 770 .. ..	..	..	24	..	..	..
Frontiera .. ..	28	..	..	..	..	..
(N.P. 770 $\times$ Frontiera) $F_1$ ..	..	..	13	..	..	..
(N.P. 770 $\times$ Frontiera) $F_2$ ..	16	..	243	259	..	..
(Observed) .. ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frontiera) $F_2$ ..	16.2	..	242.8	259	0.002	0.98 to 0.95
(expected on 1R : 15S basis) ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frontiera) $F_3$ ..	6	38	52	96	..	..
(Observed) .. ..	..	..	..	..	..	..
(N.P. 770 $\times$ Frontiera) $F_3$ ..	6	48	42	96	4.41	0.20 to 0.10
(expected on 1R : 8Seg : 7S basis) ..	..	..	..	..	..	..

TABLE 6

*Seedling reaction of the parents,  $F_1$ ,  $F_2$  and  $F_3$  of the cross, Cometa Klein  $\times$  N.P. 770, tested against race H*

Material Tested	No. of seedlings/families found			Total	$X^2$	P Value
	Resistant	Segre- gating	Sus- ceptible			
N.P. 770 .. ..	..	..	26	..	..	..
Cometa Klein .. ..	38	..	..	..	..	..
(Cometa Klein $\times$ N.P. 770) $F_1$ ..	12	..	..	..	..	..
(Cometa Klein $\times$ N.P. 770) $F_2$ (Observed) ..	137	..	130	267	..	..
(Cometa Klein $\times$ N.P. 770) $F_2$ (expected on 9R : 7S basis) ..	150.1	..	116.9	267	2.638	0.20 to 0.10
(Cometa Klein $\times$ N.P. 770) $F_3$ (Observed) ..	5	40	36	81	..	..
(Cometa Klein $\times$ N.P. 770) $F_3$ (expected on 1R : 8Seg : 7S basis) ..	5.06	40.52	35.42	81	0.017	0.99

Resistance was dominant in the  $F_1$ . The  $F_2$  and  $F_3$  breeding behaviour gave evidence of the action of two complementary gene pairs responsible for the resistance of this variety.

III. *Relationship between the genes for resistance to races 13 and H in the cross Cometa Klein  $\times$  N.P. 770:*

The behaviour of resistance to races 13 and H in the cross, Cometa Klein  $\times$  N.P. 770, being the same *i.e.* complementary action of genes (Tables 3 and 4), the reaction of the 79  $F_3$  families tested against each of the two races were examined for studying the relationship of the two pairs of genes involved in this cross. The data on the reaction of the individual families are summarised in Table 7.

TABLE 7

*Comparison of the resistance to races 13 and H of P. glumarum in 79  $F_3$  families of the cross, Cometa Klein  $\times$  N.P. 770*

Reaction to race 13			Reaction to race H			Total
			Resistant	Segregating	Susceptible	
Resistant	..	..	0	4	3	7
Segregating	..	..	2	24	23	49
Susceptible	..	..	3	10	10	23
Total	..	..	5	38	36	79

$X^2$  Value for the Test of Independence = 2.7537  
P value = 0.70 to 0.50

It will be observed from the data summarised in the above table that at least one of the two complementary genes responsible for resistance to each of these two races is not common.

#### DISCUSSION

The results reported above show that the resistance of the exotic varieties included in the present study is conditioned by one or two pairs of genes. In the cross, Frondoso  $\times$  N.P. 770, resistance was seen to be controlled by a single pair of recessive genes, while the resistance of La Prevision in its cross with Ridley was controlled by a single pair of dominant genes. Suva Ghose *et al.*, (1958) found the mature plant resistance of Cometa Klein, in crosses with susceptible Pb.C. 281 and N.P. 718, to be monofactorially dominant. The existence of a single dominant factor for resistance to yellow rust has also been reported by a number of other workers (Zapata Balcozar, 1956; Pal, 1951 and Favret and Vallega, 1953). On the other hand, resistance due to a single recessive gene has been recorded by Biffen (1907), Armstrong (1922) and Pal *et al.* (1956).

The resistance of Frontiera to race H of yellow rust in its crosses with N.P. 770 was seen to be due to the action of duplicate factors, resistance being due to the double recessive condition.



The resistance of Cometa Klein to race 13 of yellow rust in cross with N.P. 770 was due to the complementary action of two gene pairs, both of which were contributed by the resistant parent. In the same cross, resistant to race H of yellow rust was again seen to be due to the complementary action of two genes. A comparison of the breeding behaviour of the individual  $F_3$  families for their reaction to the two races, however, revealed the independent nature of at least one of the two complementary factors contributing to resistance to each of these two races of this wheat variety. This information, derived from the genetic data, is in agreement with the cytogenetic evidence collected by Singh and Swaminathan (1959). On the basis of their monosomic analysis, they found that the two genes responsible for the resistance of Cometa Klein to race H are located in Chromosomes IV and VI, whereas the single gene for resistance to race 13 located by these authors was situated on chromosome IX. But, from the genetic data reported in this paper, as also in the earlier study of Bahl and Kohli (1960), Cometa Klein was seen to possess two complementary genes for resistance to race 13 also.

The resistance of La Prevision to race 13 in the cross with N.P. 770 was seen to be controlled by a dominant gene for resistance contributed by this parent but its expression was inhibited by another dominant, epistatic gene for susceptibility contributed by N.P. 770. Pessola (1927) had also reported the resistance to yellow rust to be controlled by two genes in crosses of Extra Kolbens with a number of susceptible varieties. Pal *et al.* (1956) have, however, reported the adult plant resistance of Frondoso to yellow rust in a cross with N.P. 789 to be due to the action of three genes.

#### SUMMARY

The resistance of La Prevision to race 13 of *Puccinia glumarum* in its cross with Ridley was seen to be controlled by a single pair of dominant genes. In the cross, Frondoso  $\times$  N.P. 770, resistance to this race was due to a single pair of recessive genes. In the cross, Cometa Klein  $\times$  N.P. 770, the resistance of the Cometa Klein to race 13 was found to be governed by two pairs of complementary genes contributed by this parent. The resistance of La Prevision in its cross with N.P. 770 was due to the presence of a dominant gene, the expression which was however inhibited by a dominant epistatic gene for susceptibility contributed by the susceptible parent N.P. 770.

The resistance of Frontiera to race H of yellow rust in the cross with N.P. 770 was due to the action of duplicate factors, resistance behaving as the double recessive. However, the resistance of Cometa Klein to this race in its cross with N.P. 770, like that to race 13, was due to the complementary action of two genes present in this variety. The available evidence, however, showed that at least one of the genes involved in the resistance of Cometa Klein to these two races was not the same.

#### ACKNOWLEDGEMENTS

Acknowledgement is due to the Head of the Division of Mycology and Plant Pathology, Indian Agricultural Research Institute, New Delhi and his staff at Simla for having kindly supplied the initial inoculum of the races studied.

The authors are grateful to Dr. A. B. Joshi, Head of the Division of Botany, I.A.R.I., New Delhi for kindly going through the manuscript and offering useful suggestions regarding the presentation of the data.

The interest shown by Dr. B. P. Pal, Director, Indian Agricultural Research Institute, New Delhi, in these studies was a source of great encouragement to the authors.

## REFERENCES

- Armstrong, S. F. (1922). The mendelian inheritance of susceptibility and resistance to yellow rust (*Puccinia glumarum* E. and H.) in wheat. *J. agric. Sci.*, **12**: 57-96.
- Bahl, P. N. and Kohli, S. P. (1960). Inheritance of seedling resistance to some Indian races of yellow rust in intervarietal crosses of *Triticum aestivum*. *Indian J. Genet.*, **20**: 42-47.
- Biffen, R. H. (1907). Studies in the inheritance of disease resistance. I. *J. agric. Sci.*, **2**: 109-28.
- Favret, E. A. and Vallega, J. (1953). Inheritance of resistance to Argentine races of *Puccinia glumarum* in wheat China 166. *Phytopathology*, **43**: 471 (Abst.).
- Gassner, G. and Straib, W. (1930). Die Bestimmung der biologischen Rassen des Weizengelbrestes, *Puccinia glumarum* F. spp. *tritici* (Schmidt, Erikss. and Henn.). *Arb. biol. Abt. (Anst. Reichsanst.)*, **Berl.**, **20**: 141-63.
- Ghose, Suva, Sikka, S. M. and Rao, M. V. (1958). Inheritance studies in wheat. IV. Inheritance of rust resistance and other characters. *Indian J. Genet.*, **18**: 142-62.
- Pal, B. P. (1951). Wheat Breeding investigations at the Indian Agricultural Research Institute. *J. Indian bot. Soc.*, **30**: 1-13.
- , Sikka, S. M. and Rao, M. V. (1956). Inheritance Studies in wheat. *Indian J. Genet.*, **16**: 32-46.
- Pessola, V. A. (1927). On the inheritance of yellow rust in spring wheat. *Agric. Res., Finland*, **8**: 1-199.
- Sikka, S. M. (1955). Genetics of disease resistance and other characters in wheat and its bearing on the improvement of crop in India. *Indian J. Genet.*, **15**: 1-14.
- Singh, M. P. and Swaminathan, M. S. (1959). Mosonomic analysis in bread wheat. III. Identification of chromosomes carrying genes for resistance to two races of yellow rust in Cometa Klein. *Indian J. Genet.*, **19**: 171-75.
- Vasudeva, R. S. (1956). News from India. Yellow rust of wheat (*Puccinia glumarum*) *Commonw. Phytopath. News*, **2**: 44.
- Zapata Balcozar, M. (1956). Herencia de la 'resistencia de planta adulta de trigo' a la roya amarilla *Puccinia glumarum* (Schm.) Erikss. & Henn. bajo condiciones de campo. *Rev. Fac. nac. Agron., Columbia*, **18**: 3-63.

# GENETIC STUDIES IN BARLEY—III. LINKAGE RELATIONS OF SOME PLANT CHARACTERS

K. B. L. JAIN

*Division of Botany, Indian Agricultural Research Institute, New Delhi-12*

In previous communications, Murty and Jain (1959, 1960) reported the mode of inheritance of various plant characters. The present paper describes the linkage relations of these characters.

At present, six out of the seven possible linkage groups in barley are well established. Recent work by Kramer, Veyl and Hanson (1954) indicates that the groups formerly designated as III and VII should be considered as one. The literature on the linkage relationships in barley have been extensively reviewed by Robertson, Wiebe and Immer (1941), Robertson, Wiebe and Shands (1947, 1955) and Smith (1951).

## MATERIALS AND METHODS

The linkage relations of the following characters were studied in the  $F_2$ ,  $F_3$  and  $B_1$  generations in five crosses, *viz.*, E.B. 171  $\times$  E.B. 417, E.B. 177  $\times$  E.B. 417, K. 251  $\times$  E.B. 438, K. 251  $\times$  E.B. 132 and C. 138-2  $\times$  E.B. 132. The following symbols used for these characters are those recommended by Robertson *et al.* (1941, 1947, 1955). The asterisks indicate characters, for which recommended symbols do not appear to be available.

Non-six row <i>vs</i> six row	(V v)
Long <i>vs</i> short outer glume awns	(E e)
Normal green <i>vs</i> Virescent seedlings	(Y y, Yc yc)
Purple <i>vs</i> white leaf sheath	(Pr pr)
Hooded <i>vs</i> awned lemma	(K k)
Black <i>vs</i> white lemma and pericarp	(B b)
Semi spreading <i>vs</i> erect type of early growth habit	(Eh eh)*
Broad <i>vs</i> narrow leaves	(Brl brl)*
Early <i>vs</i> late heading date	(Ea ea, Ea <sub>2</sub> , ea <sub>2</sub> , Ea <sub>3</sub> ea <sub>3</sub> )

The association between various factor pairs was tested by  $\chi^2$  test for independence by the general contingency method. Whenever linkage was suspected the recombination value was calculated by the product method in the  $F_2$  and by the maximum likelihood method in the  $F_3$ .

## RESULTS

### A. Analysis of $F_2$ data:

(a) *Detection of linkage.*—In order to find out if there was any linkage between the various character pairs mentioned above, the joint segregation of two qualitative characters of each cross at a time were subjected to  $\chi^2$  test and that of a quantitative and a qualitative character to 't' test for independence. The results are summarized in tables 1 and 2 respectively.



TABLE 1  
*X<sup>2</sup> test for independence between various character pairs from the F<sub>2</sub> data*

Cross	Total number of plants					X <sup>2</sup>	P Value
	AB	Ab	aB	ab	Total		
<b>V v, Pr pr (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 375	29	36	90	530	227.72	<0.01
E.B. 177 × E.B. 417	.. 351	18	23	90	482	278.148	<0.01
K. 251 × E.B. 438	.. 243	30	21	61	355	132.97	<0.01
<b>V v, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 384	30	123	8	545	0.198	0.70-0.50
E.B. 177 × E.B. 417	.. 357	10	112	6	485	1.564	0.30-0.20
<b>V v, K k (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 315	132	115	47	609	0.015	0.95-0.90
C. 138-2 × E.B. 132	.. 377	104	109	25	615	0.557	0.50-0.30
<b>V v, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 337	110	127	35	609	0.592	0.50-0.30
C. 138-2 × E.B. 132	.. 360	121	102	32	615	0.091	0.80-0.70
<b>V v, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 204	72	56	28	360	1.688	0.20-0.10
<b>V v, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 206	75	68	15	364	2.555	0.20-0.10
<b>E e, Pr pr (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 287	100	123	20	530	7.380	<0.01
E.B. 177 × E.B. 417	.. 292	77	81	27	471	1.496	0.30-0.20
K. 251 × E.B. 438	.. 189	80	76	16	361	5.348	0.05-0.02
<b>E e, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 357	27	135	9	528	0.101	0.80-0.70
E.B. 177 × E.B. 417	.. 353	12	106	4	475	0.030	0.90-0.80
<b>E e, K k (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 312	138	118	41	609	1.347	0.30-0.20
C. 138-2 × E.B. 132	.. 341	90	145	39	615	0.008	0.95-0.90
<b>E e, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 343	107	121	38	609	0.001	0.98-0.95
C. 138-2 × E.B. 132	.. 332	101	130	52	615	1.605	0.30-0.20
<b>E e, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 191	80	70	19	360	2.601	0.20-0.10
<b>E e, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 207	64	67	25	363	0.468	0.50-0.30

TABLE 1—(Contd.)

Cross	Total Number of Plants					X <sup>2</sup>	P Value
	AB	Ab	aB	ab	Total		
<b>Pr pr, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 192	70	63	29	354	0.780	0.50-0.30
<b>Pr pr, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 201	68	73	18	360	1.131	0.30-0.20
<b>Pr pr, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 398	41	104	20	563	..	..
E.B. 177 × E.B. 417	.. 373	12	96	6	487	1.730	0.20-0.10
<b>K k, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 334	96	130	49	609	1.817	0.20-0.10
C. 138-2 × E.B. 132	.. 363	123	99	30	615	0.229	0.70-0.50
<b>Brl brl, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 193	88	81	12	374	12.079	<0.01

TABLE 2

‘T’ test for independence between heading date and some qualitative characters in the  $F_2$ 

Character		Mean days taken for heading	Difference	't' = $\frac{D}{S.E.D}$	't' value at 5% level
<b>Ea<sub>3</sub> ea<sub>3</sub>, V v</b>					
Non-six-row ( <b>V</b> )	..	95.3 ± 0.3293	0.7	1.06	1.959
Six-row ( <b>v</b> )	..	94.6 ± 0.5382			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Pr pr</b>					
Purple ( <b>Pr</b> )	..	94.8 ± 0.2769	0.7	1.28	1.959
White ( <b>pr</b> )	..	95.5 ± 0.5457			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Ee</b>					
Long ( <b>E</b> )	..	94.5 ± 0.3221	1.2	1.66	1.959
Short ( <b>e</b> )	..	95.7 ± 0.5713			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Br1 br1</b>					
Broad ( <b>Br1</b> )	..	95.0 ± 0.3323	0.5	0.76	1.959
Narrow ( <b>br1</b> )		95.5 ± 0.4989			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh</b>					
Semi-spreading ( <b>Eh</b> )		95.8 ± 0.3402	3.0	4.8**	1.959
Erect ( <b>eh</b> )	..	92.8 ± 0.5276			

\*\*Significant at 1 per cent level.

It would be seen that **V v** showed linkage with **Pr pr**. The loci **E e** and **Pr pr** themselves appeared to be linked in two crosses while they showed independent segregation in the third. **Eh eh** exhibited linked inheritance with **Brl brl** and **Ea<sub>3</sub> ea<sub>3</sub>**. All the other eighteen combinations studied showed that the concerned gene pairs were inherited independently of each other.

(b) *Estimation of linkage intensities*.—Whenever linkage was suspected, recombination value was worked out by the product method outlined by Immer (1930). The expected frequency distributions were calculated from the estimated cross-over values and compared with the observed values by subjecting the data to  $\chi^2$  analysis. The data showing linkage relations between various factor pairs are given in table 3.

TABLE 3

*Phenotypic distribution of F<sub>2</sub> population for different characters, from barley crosses in which linkage was suspected, with percentage recombination for each cross, as calculated by the product method*

Cross	Total number of plants					X <sup>2</sup>	P value
	AB	Ab	aB	ab	Total		
V v, Pr pr							
(i) <i>E.B. 171 × E.B. 417 (Coupling phase)</i>							
F <sub>2</sub> observed ..	375	29	36	90	530		
Expected							
(11.8±1.50%) ..	368.07	29.43	29.43	103.07		3.621	0.50–0.30
(ii) <i>E.B. 177 × E.B. 417 (Coupling phase)</i>							
F <sub>2</sub> observed ..	351	18	23	90	482		
Expected							
(9.2±1.38%) ..	340.34	21.16	21.16	99.34		1.840	0.70–0.50
(iii) <i>K. 251 × E.B. 438 (Coupling phase)</i>							
F <sub>2</sub> observed ..	243	30	21	61	355		
Expected							
(15.3±2.09%) ..	241.17	25.08	25.08	63.67		1.755	0.70–0.50
E e, Pr pr							
(i) <i>E.B. 171 × E.B. 417 (Repulsion phase)</i>							
F <sub>2</sub> observed ..	287	100	123	20	530		
Expected							
(39.2±3.63%) ..	285.35	112.15	112.15	20.35		2.436	0.50–0.30
(ii) <i>K. 251 × E.B. 438 (Repulsion phase)</i>							
F <sub>2</sub> observed ..	189	80	76	16	361		
Expected							
(40.2±3.48%) ..	194.98	75.62	75.62	14.58		0.5773	0.95–0.90
Brl brl, Eh eh							
(iii) <i>K. 251 × E.B. 438 (Repulsion phase)</i>							
F <sub>2</sub> observed ..	193	88	81	12	374		
Expected							
(34.5±4.52%) ..	198.13	82.37	82.37	11.13		0.608	0.90–0.80



It will be seen that the cross-over values between **v-pr**, worked out in the three crosses, ranged from 9.2 per cent. to 15.3 per cent. The linkage intensities between **e-pr**, in the two crosses were 39.2 per cent. and 40.2 per cent. The gene **eh** showed linkage with **brl** at a distance of 34.5 per cent. cross-over value. It also showed a significant association with **ea<sub>3</sub>**.

#### B. Analysis of back-cross data

The association between the factor pairs **V v K k**, **V v B b**, **K k B b** and **V v Pr pr** was studied from the backcross data. The results are set out in table 4.

TABLE 4

*X<sup>2</sup> test for independence between various characters from the test cross data*

Cross	Total number of plants					X <sup>2</sup>	P value
	AB	Ab	aB	ab	Total		
V v, K k							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	22	30	25	25	102	
Expected							
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		1.284 0.80-0.70
V v, B b							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	28	24	19	31	102	
Expected							
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		3.177 0.50-0.30
K k, B b							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	21	26	26	29	102	
Expected							
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		1.284 0.90-0.70
V v, Pr pr							
(E.B. 171 × E.B. 417) F <sub>1</sub> × E.B. 171							
Observed	..	7	1	2	9	19	
Expected							
(1 : 1 : 1 : 1)	..	4.75	4.75	4.75	4.75		9.38 0.05-0.02

There was no linkage between the loci studied in the back cross, (K. 251 × E.B. 132) × K. 251. In the other backcross, (E.B. 171 × E.B. 417) × E.B. 171, **V v** and **Pr pr** appeared to be linked with a recombination value of 15.8 per cent (Table 5).

TABLE 5

*Phenotypic distribution with percentage recombination, of  $B_1$  population for  $V v, Pr pr$  from the back-cross ( $E.B. 171 \times E.B. 417$ )  $F_1 \times E.B. 171$*

Material	Total number of plants					$X^2$	P Value
	AB	Ab	aB	ab	Total		
Observed ..	7	1	2	9	19		
Expected ( $15.8 \pm 8.41\%$ ) ..	6.83	2.67	2.67	6.83		1.532	0.70-0.50

### C. Analysis of $F_3$ data

(a) *Detection of linkage.*—The linkage relationship between various factor pairs was studied in the different crosses from the  $F_3$  data. In all, nineteen character combinations were studied in this generation. The observed frequencies for various genotypes, with the  $\chi^2$  test for independence are given in table 6.

TABLE 6

*$X^2$  test for independence between genes for various characters, from  $F_3$  data*

Material	Total number of families										X <sup>2</sup>	P value	
	AA BB	Aa BB	AA Bb	Aa Bb	AA bb	Aa bb	aa BB	aa Bb	aa bb	Total			
Vv, Pr pr (1:2:1) (1:2:1)													
E.B. 171 × E.B. 417	..	17	13	3	29	0	4	1	6	26	99	79.38	<0.001
E.B. 177 × E.B. 417	..	23	7	4	29	1	5	2	10	17	98	65.10	<0.001
Vv, Yc yc (1:2:1) (1:2)													
E.B. 171 × E.B. 417	..	9	17	11	29	..	..	10	23	..	99	1.17	0.70-0.50
E.B. 177 × E.B. 417	..	11	17	17	23	..	..	11	19	..	98	0.26	0.90-0.80
Vv, K k (1:2:1) (1:2:1)													
K. 251 × E.B. 132	..	10	8	12	22	3	10	9	9	7	90	5.42	0.30-0.20
C. 138-2 × E.B. 132	..	5	10	5	25	4	12	4	10	5	80	1.86	0.80-0.70
Vv, B b (1:2:1) (1:2:1)													
K. 251 × E.B. 132	..	5	8	11	24	9	8	8	12	5	90	5.17	0.30-0.20
C. 138-2 × E.B. 132	..	3	18	7	22	4	7	5	11	3	80	2.81	0.70-0.50
Vv, Eh eh (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	1	2	5	10	1	7	5	8	0	39	6.71	0.20-0.10
Vv, Br1 br1 (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	3	13	10	18	3	11	4	10	8	80	3.32	0.70-0.50
Vv, Ea <sub>3</sub> ea <sub>3</sub> (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	1	2	5	10	1	7	5	8	0	39	6.71	0.20-0.10

TABLE 6—(Contd.)

Material	Total number of families										X <sup>2</sup>	P value	
	AA BB	Aa BB	AA Bb	Aa Bb	AA bb	Aa bb	aa BB	aa Bb	aa bb	Total			
E e, Pr pr (1:2:1) (1:2:1)													
E.B. 171 × E.B. 417	..	3	14	16	18	15	9	14	4	6	99	21.43	<0.001
E.B. 177 × E.B. 417	..	10	13	8	22	7	10	7	9	5	91	1.64	0.90-0.80
E e, Yc yc (1:2:1) (1:2)													
E.B. 171 × E.B. 417	..	9	17	11	29	..	..	10	23	..	99	1.18	0.50-0.30
E.B. 177 × E.B. 417	..	13	17	12	28	..	..	6	15	..	91	3.61	0.20-0.10
E e, Kk (1:2:1) (1:2:1)													
K. 251 × E.B. 132	..	6	14	9	22	7	8	7	11	5	89	1.57	0.90-0.80
C. 138-2 × E.B. 132	..	5	6	4	24	6	12	7	13	3	80	7.16	0.20-0.10
E e, Bb (1:2:1) (1:2:1)													
K. 251 × E.B. 132	..	6	8	13	23	3	13	7	10	6	89	3.18	0.70-0.50
C. 138-2 × E.B. 132	..	4	15	6	19	5	8	7	15	1	80	6.36	0.20-0.10
E e, Eh eh (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	3	3	4	12	3	4	2	7	1	39	2.48	0.70-0.50
E e, Brl brl (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	7	6	10	22	8	10	7	6	4	80	5.15	0.30-0.20
E e, Ea <sub>3</sub> ea <sub>3</sub> (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	6	15	17	16	2	7	5	7	5	80	6.22	0.20-0.10
Pr pr, Yc yc (1:2:1) (1:2)													
E.B. 171 × E.B. 417	..	16	12	15	26	..	..	8	22	..	99	84.71	0.10-0.05
E.B. 177 × E.B. 417	..	14	14	18	29	..	..	11	12	..	98	2.53	0.30-0.20
Kk, Bb (1:2:1) (1:2:1)													
K. 251 × E.B. 132	..	8	6	11	28	8	9	7	8	5	90	6.56	0.20-0.10
C. 138-2 × E.B. 132	..	5	11	13	19	8	10	2	9	3	80	1.87	0.80-0.70
Ea <sub>3</sub> ea <sub>3</sub> , Brl brl (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	8	14	6	20	6	4	4	14	4	80	7.27	0.20-0.10
Ea <sub>3</sub> ea <sub>3</sub> , Eh eh (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	1	4	9	11	6	3	3	2	0	39	9.31	Just 0.05
Brl brl, Eh eh (1:2:1) (1:2:1)													
K. 251 × E.B. 438	..	3	1	2	14	3	2	5	6	3	39	9.99	0.05-0.02



The  $F_3$  data supplied added information concerning the apparent linkage or independence of the various character combinations. The results obtained in this generation were similar to those obtained in the  $F_2$  generation.

It will be seen from Table 6 that there was an indication of linkage between factor pairs **V v**, **Pr pr** in two crosses; between **E e**, **Pr pr** in one of the two crosses and between **Eh eh**, **Ea<sub>3</sub> ea<sub>3</sub>** and between **Brl brl**, **Eh eh**. The other factor combinations showed independent segregation.

(b) *Estimation of linkage intensities*.—In the crosses where there was an indication of linkage, the recombination values were worked out by the maximum likelihood method for the doubly dominant  $F_2$  phenotypes, classified into genotypes in the  $F_3$ . The equation to be maximized by differentiation with respect to 'p' from doubly dominant  $F_2$ s (AB), is given by Kramer and Burnham (1947).

The linkage intensities for the different character combinations in various crosses, as worked out from the  $F_3$  data, are set out in table 7.

TABLE 7

*Values of p calculated by the maximum likelihood method from the  $F_3$  data, together with their standard errors*

Source of data		Percentage recombination
<b>V v, Pr pr</b>		
E.B. 171 × E.B. 417	.. ..	20.0 ± 5.12
E.B. 177 × E.B. 417	.. ..	13.5 ± 4.06
<b>E e, Pr pr</b>		
E.B. 171 × E.B. 417	.. ..	43.5 ± 10.01
<b>Brl brl, Eh eh</b>		
K. 251 × E.B. 438	.. ..	43.0 ± 15.96
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh</b>		
K. 251 × E.B. 438	.. ..	38.0 ± 12.53

It will be seen from Table 7 that the linkage between the genes **V v**, **Pr pr** was 20.0 per cent. in the cross E. 171 × E.B. 417 and 13.5 per cent. in the cross E.B. 177 × E.B. 417. The genes **E e**, **Pr pr** were linked with a cross-over value of 43.5 per cent. The genes **Brl brl** showed linkage with **Eh eh** with a cross-over value of 43.0 per cent. and with **Ea<sub>3</sub> ea<sub>3</sub>** with a cross-over value of 38.0 per cent.

#### D. Combined linkage intensity values

The linkage intensities for different factor pairs obtained from different sources, viz.,  $B_1$ ,  $F_2$  and  $F_3$  generations, and from various crosses, were combined and an average p value worked out. Fisher's method of scoring (1946) was adopted to test the

homogeneity of the group of linkage intensities to be combined. When the data were considered homogeneous, the average *p* value was obtained by approximating the combined *p* value by weighting each separate recombination value by appropriate use of the amount of information furnished by each source of data.

The recombination percentages obtained from various sources of data, their test for homogeneity and the average *p* value, as determined from all the data combined, are summarized in table 8.

TABLE 8

*X*<sup>2</sup> test for homogeneity of different *p* values from various sources and the average weighted *P* values

Source of material	Percentage recom- bination			X <sup>2</sup> for homoge- neity	D.F.	P value from X <sup>2</sup> for homo- geneity	Average percentage recombina- tion by weigh- ting
	F <sub>2</sub>	F <sub>3</sub>	B <sub>I</sub>				
V v, Pr pr							
E.B. 171 × E.B. 417 ..	11.8	20.0	15.8				
E.B. 177 × E.B. 417 ..	9.2	13.5	..	7.72	5	0.20-0.10	11.74±0.3
K. 251 × E.B. 438 ..	15.3	..	..				
E e, Pr pr							
E.B. 171 × E.B. 417 ..	39.2	43.5	..				
K. 251 × E.B. 438 ..	40.2	..	..	0.109	2	0.95-0.90	39.88±2.59
Brl brl, Eh eh							
K. 251 × E.B. 438 ..	34.5	43.0	..	1.674	1	0.20-0.10	35.12±4.32
Ea <sub>3</sub> ea <sub>3</sub> , Eh eh							
K. 251 × E.B. 438 ..	Corre- lated	38.0	..	..	..	..	38.0±12.53

## DISCUSSION

The work done by previous workers indicates that the factors **V v**, **E e**, **Pr pr**, **B b** and **K k** are located in linkage groups I, I, I, II and IV respectively (Ubisch, 1919; Miyake and Imai, 1929; Robertson, 1929; Buckley, 1930; Daane, 1931 and others). The factors for normal *vs* virescent seedlings have been located in two linkage groups, I and VII and have been designated as **Y y** and **Yc yc** respectively (Robertson *et al.* 1941). In the present study, the normal *vs*. virescent seedling character did not show any linkage with **V v**, **E e** and **Pr pr**, reported to be located in linkage group I. The factor controlling virescence of E.B. 171 and E.B. 177 is, therefore, likely to be located in linkage group VII. This, however, needs confirmation by studying the relationship of this factor with the marker genes of group VII.

The fact that the factors **V v**, **E e** and **Pr pr** are located in the linkage group I, as observed by a number of other workers, is confirmed by the results obtained in the

present study. These factors appeared to be linked with each other, the cross-over values between **v-pr**, and **e-pr** being 11.74 per cent. and 39.9 per cent. respectively. Between **v-pr**, Robertson (1933) calculated the recombination value to be 9.0 per cent. Woodward (1957) reported this value to be 16.0 per cent. Between **v-e**, the recombination values reported by different workers were 26.6 per cent. (Robertson, Immer, Wiebe and Stevenson, 1944), 24.7 per cent. (Bose, Aziz and Bhatnagar, 1937), 28.0 per cent. (Immer and Henderson, 1943), and 26.7 per cent. (Swenson and Wells, 1944). Woodward (1957) studied five crosses with regard to these factor pairs and found that in four crosses the linkage values ranged from 26.5 to 27.0 per cent., while in the fifth cross there was no linkage between these characters. In the present study also such a situation has been met with. The reasons for such a discrepancy are, however, not quite clear from the data available in this study, though several reasons have been suggested (Woodward, 1957). The information on the linkage relationship between the factors **e-pr** does not seem to be reported in the literature so far.

The factors **eh-brl** and **eh-ea<sub>3</sub>** showed linkage with cross-over values of 35.12 per cent. and 38.0 per cent. respectively, while **ea<sub>3</sub>** and **brl** appeared to show independent inheritance from each other. These data, therefore, suggest that the order of these three genes is **ea<sub>3</sub>-eh-brl**. Information on the linkage relationships of these genes are being reported for the first time. These genes were found to be inherited independently of the factors on chromosome I.

Factors for heading date have been located in three linkage groups, viz. I, IV and V and have been designated as **Ea ea**, **Ea<sub>2</sub> ea<sub>2</sub>** and **Ea<sub>3</sub> ea<sub>3</sub>** respectively (Griffie, 1925; Neatby, 1929 and Robertson *et al.*, 1947). In the present study, heading date did not show any linkage with **V v**, **E e** and **Pr pr** of group I. This, therefore, suggests that the factor **Ea ea** does not operate in controlling the expression of heading date in the cross under study. The factor controlling this character in this cross may, therefore, be located in linkage group IV or V. The factor controlling semi-spreading *vs* erect type of early growth habit (**Eh eh**) does not seem to have been studied previously although information is available on the factors controlling spring *vs*. winter habit. Three independent factors, viz., **Sh sh**, **Sh<sub>2</sub> sh<sub>2</sub>** and **Sh<sub>3</sub> sh<sub>3</sub>**, have been reported to control the expression of this character. Takahashi and Yasuda (1956) showed that the factor pair **Sh<sub>2</sub> sh<sub>2</sub>** is linked with **R r** for awn barbing and **S s** for rachilla hairs in the order **Sh<sub>2</sub>-r-s**, in linkage group V. Walker, Kasha and Miller (1958) have reported that the factor for broad leaves is linked with the factor controlling long *vs*. short-haired rachilla (**S s**) in linkage group V. If it is considered that the factor controlling the leaf shape (**Brl brl**) in the cross under study is the same as that reported by Walker *et al.* (1958) and is located on chromosome V, then the factors for heading date and early growth habit can be located on chromosome V, as they show linkage with the factor for leaf shape, their order of arrangement being **ea<sub>3</sub>-eh-brl**. However, the assumption that these genes lie on chromosome V needs further confirmation by studying their relationship with other marker genes in linkage group V.

#### SUMMARY

Linkage relationships between twenty-two character combinations were studied in the different crosses of barley in the F<sub>2</sub>, F<sub>3</sub> and B<sub>1</sub> generations.

The factors controlling the expression of normal *vs*. virescent seedlings (**Yc yc**), hoods *vs*. awns (**K k**), black *vs*. white lemma and pericarp (**B b**), broad *vs*. narrow leaves (**Brl brl**) and heading date (**Ea<sub>3</sub> ea<sub>3</sub>**) showed independent inheritance from the factors for non-six row *vs*. six row (**V v**) and long *vs*. short outer glume awns (**E e**). The factors **Eh eh**, **Brl brl**, **Ea<sub>3</sub> ea<sub>3</sub>** and **Yc yc** were inherited independently of **Pr pr** (purple *vs*. white leaf sheath). The factor **K k** also showed independent inheritance from **B b** factor,



It appears that the factors **V**, **e** and **pr** belong to linkage group I, the cross-over values among **v-pr** and **e-pr**, being  $11.74 \pm 0.87$  per cent and  $39.88 \pm 2.69$  per cent respectively.

The cross-over values between the genes **eh-brl**, **eh-ea<sub>3</sub>** were  $35.12 \pm 4.32$  per cent. and  $38.0 \pm 12.53$  per cent. respectively, while **ea<sub>3</sub>** and **brl** appeared to show independent inheritance. The order of these genes, therefore, appears to be **ea<sub>3</sub>-eh-brl**; none of these genes showed any linkage with marker genes in linkage group I. The possibility of these genes belonging to linkage group V is discussed.

#### ACKNOWLEDGEMENTS

I am grateful to Dr. S. M. Sikka, formerly Head of the Division of Botany, and Dr. G. S. Murty, formerly Wheat Breeder, for their encouragement and keen interest in the study. My thanks are due to Dr. A.B. Joshi, Head of the Division of Botany, for critically going through the manuscript and making valuable suggestions.

#### REFERENCES

- Bose, R. D., Aziz, M. S. and Bhatnagar, M. P. (1937). Studies in Indian barleys. IV. The inheritance of some anatomical characters responsible for lodging and of some ear-head characters in an interspecific cross between two Pusa barleys. *Indian J. agric. Sci.*, **7**: 48-88.
- Buckley, G. F. H. (1930). Inheritance in barley with special reference to the colour of caryopsis and lemma. *Sci. Agric.*, **10**: 460-92.
- Daane, A. (1931). Linkage relations in barley. *Tech. Bull. Minn. Agric. Exp. Sta.*: 78.
- Fisher, R. A. (1946). A system of scoring linkage data, with special reference to the pied factors in mice. *Amer. Nat.*, **80**: 568-78.
- Griffiee, F. (1925). Correlated inheritance of botanical characters in barley and manner of reaction to *Helminthosporium sativum*. *J. agric. Res.*, **30**: 915-35.
- Immer, F. R. (1930). Formulae and tables for calculating linkage intensities. *Genetics*, **15**: 81-98.
- and Henderson, M. T. (1943). Linkage studies in barley. *Genetics*, **28**: 419-40.
- Kramer, H. H. and Burnham, C. R. (1947). Methods of combining linkage intensity values from back-cross,  $F_2$  and  $F_3$  genetic data. *Genetics*, **32**: 379-90.
- and Veyl, R. and Hanson, W. D. (1954). The association of two genetic linkage groups in barley with one chromosome. *Genetics*, **39**: 159-68.
- Miyake, K. and Imai, Y. (1922). Genetic studies in barley. *Bot. Mag. (Tokyo)*, **36**: 25-38 from Buckley, *Sci. Agric.*, **10**: (1930).
- Murty, G. S. and Jain, K. B. L. (1959). Genetic studies in barley. I. Inheritance of pigmentation in various plant parts. *Indian J. bot. Soc.*, **38**: 561-74.
- , (1960). Genetic studies in barley. II. Inheritance of fertility of the lateral florets and certain other characters. *Indian J. bot. Soc.*, **39**: 281-308.
- Neatby, K. W. (1929). An analysis of the inheritance of quantitative characters and linkage in barley. *Sci. Agric.*, **9**: 701-18.
- Robertson, D. W. (1929). Linkage studies in barley. *Genetics*, **14**: 1-36.
- (1933). Inheritance in barley. *Genetics*, **18**: 148-58.
- Wiebe, G. A. and Immer, F. R. (1941). A summary of linkage studies in barley. *J. Amer. Soc. Agron.*, **33**: 47-64.
- , and Shands, R. G. (1947). A summary of linkage studies in barley. Suppl. I. 1940-1946. *J. Amer. Soc. Agron.*, **39**: 464-73.
- , (1955). A summary of linkage studies in barley. Suppl. II. 1947-53. *Agron. J.*, **47**: 418-25.
- Immer, F. R., Wiebe, G. A. and Stevens, H. (1944). The location of two genes for mature plant characters in barley linkage group No. 1. *J. Amer. Soc. Agron.*, **36**: 66-72.
- Smith, L. (1951). Cytology and genetics of barley. *Bot. Rev.*, **17**: 1-51, 133-202, 285-355.
- Swenson, S. P. and Wells, D. G. (1944). The linkage of four genes in chromosome I of barley. *J. Amer. Soc. Agron.*, **36**: 429-35.
- Takahashi, R. and Yasuda, S. (1956). Genetic studies of time of heading in barley. *Proc. Int. Genetics Symposia. Tokyo & Kyoto*: 498-501.
- Ubisch, G. von (1919). Beitrag in einer Fakteranalyse von gertse II. *Z. induk. Abstam. U.-Vererblehre.*, **20**: 65-117.
- Walker, G. W. R., Kasha, K. and Miller, R. A. (1958). Recombination studies in barley. *Proc. Genet. Soc. Canada*, **3**: 41-43.
- Woodward, R. W. (1957). Inheritance studies in barley. *Agron. J.*, **49**: 28-32.

## STUDIES ON WORLD GENETIC STOCK OF RICE (*ORYZA SATIVA* L.)— II. AWNING

B. MISRO, R. SEETHARAMAN and R. H. RICHHARIA

*Central Rice Research Institute, Cuttack*

AWN is the pointed protrusion of the apiculus and is a continuation of the middle nerve of the lemma. Awning is commonly found in almost all wild rices and is not uncommon in cultivated rices. This has its own advantages, in that it ensures against damage by birds and also, to some extent, by field rats. But, the growers do not generally prefer the awned types, as these are difficult to handle and give less weight of grain than awnless types, taken volume to volume. The millers also prefer awnless types to awned ones.

Environmental influence on awning has been reported by several workers. Anandan (1933) records that close spacing and manuring increase not only the percentage of awned grains in a panicle, but also the length of the individual awns. Sethi *et al.* (1937) report a similar experience with close spacing, but did not observe any effect of manuring on awning. Mendiola (1926) records that awn development is augmented by plentiful supply of water. Sometimes, the same plant has been observed to have awned spikelets in the secondary and tertiary tillers, but none in the primary ones. Sahadevan (1959) observes that an awnless variety develops awns when ratooned and that root pruning inhibits awning in an awned variety, indicating that a physiological balance between root and shoot development is influencing the expression of awning.

Despite such environmental influence on its expression, awning is known to be genetically controlled and has been used as one of the criteria in the classification (Chatterjee, 1948) of species of *Oryza*. Hutchinson and Ramiah (1938) grouped awned types into three categories, *viz.*, tipped, awned and fully awned. Apart from the above three groups, intermediate forms are also observed in any segregating population from awned  $\times$  awnless crosses. It would, therefore, appear that besides major genes, polygenes also influence awning.

In the present paper, the occurrence of awning in rice, as observed in the Genetic Stock maintained at the Central Rice Research Institute, is reported. The intensive collection made in connection with the Botanical Survey of the Jeypore Tract of Orissa (India), supposed to be one of the secondary centres of origin of rice, has also been studied for this character. It may be mentioned that there has been little human interference in this area.

### MATERIALS AND METHODS

Varieties in which almost all the spikelets in the panicle possess long awns are taken as awned. Those in which only a few spikelets in the panicle possess short awns are termed as tipped. Material from the Genetic Stock, built up from different countries has been considered as improved types, as opposed to indigenous types, collected from the Jeypore Tract.

### RESULTS

In table 1 is furnished the distribution of awned types in the two different rice-growing regions of the World, based on the latitude of the countries, from which the material under observation has been obtained.

TABLE 1

*Distribution of awning in the Genetic Stock and Jeypore collection of rice*

Region	Genetic Stock			Jeypore Collection	
	Awn class	Frequency	Percentage	Frequency	Percentage
23½° N to 23½° S	Awned	72	4.3	183	10.5
	Tipped	133	7.9	60	3.4
	Awnless	1,466	87.8	1,499	86.1
	Total ..	1,671	100.0	1,742	100.0
23½° N to 40° N and 23½° S to 40° S	Awned	64	7.1	..	..
	Tipped	68	7.5	..	..
	.. Awnless	769	85.4	..	..
	Total ..	901	100.0	..	..
Grand Total ..		2,572*		1,742	

The distribution of awned varieties in the tropical and the temperate regions is thus different ( $\chi^2=9.2$  with 2 d.f.; P bet. 0.02 and 0.01).

## DISCUSSION

In the Jeypore collection, the percentage of awned types is 10.5 and is low compared with the awnless types (86.1 per cent). It may, therefore, be concluded that the awnless condition might have occurred very early in the evolutionary history of cultivated rice. The value of 10.5 per cent. obtained for awned types in the Jeypore material against 4.3 per cent. obtained for the Genetic Stock material (improved) shows that human interference has been least in the former material. This lends support to the contention that Jeypore area is one of the secondary centres of origin of cultivated rice.

The genetic stocks collected from the tropical and temperate regions of the world differ significantly from each other in the frequency of occurrence of awned types. It appears that there is a higher frequency of such types in the temperate belt. Distribution of awn in the varieties also indicates certain features. Most of the wild types (generally hardy) possess awns. The salt-resistant and flood-resistant types barring a few exceptions also possess awns. The non-lodging *bulu* types of Indonesia are all awned, as also some of the non-lodging varieties. Ramiah (1953) records that the hardy *aman* types of Assam, grown under deep water conditions, as well as the drought-resistant summer rice (*boro*) are awned. Thus, awning is associated with hardiness, general vigour, drought resistance etc. The exact nature of the association is, however, not clear.

The growth and development of the rice plant seem to have an intimate relationship with the development of awning, which is another growth process. Preliminary studies by Sahadevan (1959) show that there is a certain physiological balance between shoot and root development, which affects the expression of awning.



It would appear that in the tipped types, some sort of a compromise or physiological balance has been attained between awnedness and awnlessness. This has been taken advantage of, consciously or unconsciously, and as a result in the tropics as well as in the subtropics, tipped types are numerically more than awned types. Such a preponderance of tipped types over awned types has also been observed by Jones (1927).

Genetical studies in awning conducted by different workers have shown that one to three major genes are involved in the expression of awning. However, it is commonly observed that the nature of variation in awning is continuous in any population segregating for this character. From these observations, it may be inferred that a system of polygenes besides one or more pairs of major genes govern awning. Accordingly, the awnless types could be due to either (i) the presence of only polygenes, each one contributing a little towards the increased expression of awning, but the combined effect not being phenotypically identifiable (**an an**++++...) (ii) the presence of dominant major gene or genes combined with polygenes, each contributing a little to the decreased expression of awning (**An An**-----...) or (iii) the presence of only polygenes, each contributing a little to the decreased expression of awning (**an an**-----...). Likewise, the genotypic constitution of any awned type can be different.

It is known that awning appears in the autotetraploid of most phenotypically awnless diploids. Such diploids could be of the constitution (**an an**++++...). Further, doubling the chromosome complement of diploids with the genotype (**an an**-----...) would not result in the expression of awns at the tetraploid level.

In a cross between two genotypes of the constitutions (**An An**-----...) and (**an an**++++...) respectively, the  $F_1$  hybrid would show awning (*e.g.*, Shah, 1955).

Whether the loci of the major genes, involved in the expression of awning, are the same in both the cultivated rices *viz.*, *Oryza sativa* and *O. glaberrima* is yet to be ascertained. If the loci involved are different, the difference in awning would be due to two pairs of major genes. Studies, carried out by Gopalakrishnan (1959), have shown the existence of polygenic system in some of the African forms.

The knowledge regarding awning and its expression is as yet incomplete and further studies are needed to throw light on the different aspects of awning.

#### SUMMARY

A survey of the World Genetic Stock of rice and the collection from Jeypore tract in Orissa State shows that (i) the percentage of awned varieties under cultivation is as low as 4.3 and (ii) the mutation for awnless condition is likely to have occurred very early in the evolutionary history of rice.

Awning appears to be mostly associated with hardiness, drought resistance, salt resistance, non-lodging habit etc. The predominance of tipped types in the cultivated rices is taken to indicate that, in these types, a physiological balance has been reached between general hardiness and the other advantages associated with awning on the one hand and certain desirable characters possessed by the awnless types on the other.

It is suggested that awning is governed by the action of major gene or genes and a polygenic system, thus explaining the continuous variation so commonly observed in any population segregating for awning.

#### ACKNOWLEDGEMENTS

We are thankful to Sri S. Sampath, Cytologist for his valuable suggestions and to Dr. S. Govindaswamy, Assistant Botanist, Jeypore Botanical Survey Scheme for

making available the data on Jeypore collection. The authors are also grateful to Dr. K. Ramiah, F.A.O. Rice Expert (Retd.), for going through the manuscript critically and for making valuable suggestions.

## REFERENCES

- Anandan, M. (1933). *Madras Agric. Stn. Rept., Aduthurai* (1932-33): 14-17.
- Chatterjee, D. (1948). A modified key and enumeration of the species of *Oryza* Linn. *Indian J. agric. Sci.*, **18**: 185-92.
- Gopalakrishnan, R. (1959). *Cytogenetical studies on interspecific hybrids in the genus, Oryza*. Unpublished Thesis for Assoc. I.A.R.I., Indian Agric. Res. Inst., New Delhi.
- Hutchinson, J. B. and Ramiah, K. (1938). Description of crop plant characters and their ranges variation. II. Variability in rice. *Indian J. agric. Sci.*, **8**: 592-616.
- Jones, J. W. (1927). Inheritance of awnedness in rice. *J. Amer. Soc. Agron.*, **19**: 830-39.
- Mendiola, N. B. (1926). *A manual of plant-breeding in the tropics*. University Press, Manila.
- Ramiah, K. (1953). *Rice Breeding and Genetics*. Indian Council of Agricultural Research, New Delhi, Scientific Monograph, 19.
- Sahadevan, P. C. (1959). Studies on the developmental variation of awn in rice. *Curr. Sci.*, **28**: 491-92.
- Sethi, R. L., Sethi, B. L. and Mehta, T. R. (1937). Awnedness and its inheritance. *Indian J. agric. Sci.*, **7**: 589-600.
- Shah, S. S. (1955). *Morphological and anatomical studies in the genus Oryza*. Unpublished Thesis for Assoc. I.A.R.I., Indian Agric. Res. Inst., New Delhi.

# GENETICS OF PHOTOPERIOD RESPONSE IN RICE

S. SAMPATH and D. V. SESHU

*Central Rice Research Institute, Cuttack*

DURING the course of an investigation on the genetic differences between the *japonica* and *indica* sub-species of rice, a significant feature was noted in the  $F_1$  hybrids of these two sub-species with regard to photoperiodic response. The  $F_1$  hybrids in general proved capable of flowering and setting seed throughout the year when propagated by stubbles or ratoons. It was well established that the *indica* parental varieties included in the present investigations were those which normally do not flower under the long day conditions at Cuttack from April to October and might be considered short-day plants. Since the *japonica* parents were not sensitive to photoperiod, it seemed that the character of *japonica* parents was dominant over that of the *indica* parents. Such a dominance of insensitivity (period-fixed) over sensitivity (season-bound) had been recorded by Srinivasan (Quoted by Ramiah and Rao, 1953) in inter-*indica* hybrids. But this is seemingly contradictory to the findings of Chandraratna (1955) who had conducted critical experiments on the genetics of photoperiod response in rice and therefore, a series of experiments were started at the Central Rice Research Institute and the first two years' results are presented below.

## MATERIALS AND METHODS

Three *japonica* varieties viz., *Gaisen Mochi*, *Fukoku* and *Zuihio* were used as parents in these studies. These three varieties behave as period-bound (photo-insensitive) varieties at Cuttack, flowering in 50 to 75 days of sowing, irrespective of the date of sowing. Fifteen *indica* varieties from India, Burma, Malaya, Indo-china and Philippines, selected at random, were used as the *indica* parents. These varieties were of different flowering duration ranging from 110 to 130 days but they were alike in being short-day plants (photo-sensitive) i.e., flowered only in October or November, irrespective of whether they were sown in May, June or July. Two other types, a short duration *indica* named *Hastikalmi* and a wild rice classified as *Oryza perennis* were also used in this study. The work done in 1955-56 showed that the subject of flowering response of rice plant to changes in day-length was complex and that results could be obtained only by restricting the scope of the experiment and by devising suitable techniques. Since a sufficiently large area with facilities for controlling light could not be secured, the technique was restricted to the use of natural variation in day-lengths at Cuttack from January to December. The day-length (excluding twilight) begins to increase above 12 hours after summer equinox on 21st March and falls below 12 hours after winter equinox on 21st September.

Rice plants begin to be sensitive to photoperiods after a basic vegetative growth of 25 to 35 days. The photoperiod induction phase is about 20 days under suitable temperature conditions and panicle differentiation and emergence takes another 15 to 25 days. A rice plant flowering on 5th April would have formed the primordia by 20th March and this differentiation would have taken place under the photoperiods, prevailing from 1st to 20th March, which are short days. It was established that when ratooning or stubble propagation was adopted, the flowering of the tiller depends on the day-lengths prevailing at the time of the development of the tiller and not on the previous history of the plant. That is, a short-day plant ratooned in May will flower only in October, but when ratooned in October will flower in November.



Using these established features of the rice plant, the photoperiod character studied was whether a plant of given genetic constitution could flower under long day conditions prevailing in the months of May, June, July and August. Those capable of flowering under long day-lengths were termed insensitive and those flowering under only short day-lengths, sensitive.

Stubbles of  $F_1$  hybrids were cut and propagated every month of the year and the time of panicle emergence noted. It was found that with suitable precautions this procedure could be adopted indefinitely. For testing  $F_2$  behaviour, seeds from  $F_1$  plants were germinated by 1st April and transplanted in the field in the 1st week of May. The number of plants that flowered upto 1st September out of the total population for each combination was counted. The segregating ratios of flowered to non-flowered plants were considered equivalent to ratios of non-sensitive to sensitive plants. In the following year an experiment in ratooning of two  $F_2$  populations was done. The shoots were cut completely, bimonthly and the ratios between flowering and non-flowering plants were recorded as before.

### RESULTS

The hybrid between two insensitive varieties, *Fukoku (japonica)* and *Hastikalmi (indica)* was insensitive and the  $F_2$  progeny were all insensitive, all flowering before September.

The  $F_1$  hybrids between *Fukoku (japonica)* and 11 sensitive *indica* types were insensitive, and the ratoon crops established in April, flowered freely in May. With these hybrids, an unexplained observation was made. There was a cessation of flowering with the onset of monsoon in June, July flowering was sparse and August flowering was normal. The  $F_1$  hybrids between the *japonica* variety, *Zuihio* and a similar set of sensitive *indica* varieties were sensitive and the ratoon crops failed to flower between April and the middle of September. The segregation for sensitiveness in the  $F_2$  populations of these hybrids is presented briefly in table 1a.

The ratios obtained show definite consistency. The experiments have to be repeated in detail and the genetics of selected  $F_3$  populations also studied, before a valid interpretation of the number of genes involved can be made. The data presented, however, definitely show the trend of inheritance and dominance. Table 1a indicates that insensitiveness is dominant when *Fukoku* is used as a parent. The  $F_2$  ratios are either 15 : 1 or 3 : 1 for insensitivity. The variety *Zuihio* has been recorded as being sensitive to photoperiods in Japan (Morinaga and Kuriyama 1954). However, it flowers as an insensitive variety at Cuttack and therefore, it can be termed, partly-sensitive. Under high temperatures and not too long days in the tropics, it is insensitive—*Zuihio*  $\times$  *indica* hybrids must be considered as crosses between *partly-sensitive*  $\times$  *sensitive* varieties. In these crosses, the  $F_1$  is sensitive and in the  $F_2$  sensitiveness is dominant. *Zuihio* and *Fukoku* differ only slightly in their duration at Cuttack (Table 1b) but on hybridisation with sensitive *indicas*, their different genetic make up with regard to sensitiveness is brought out.

A check of dominance relationship was obtained by using ratoon crops of  $F_2$  populations. The crosses used were *Fukoku*  $\times$  *B.A.M. 9* and *Fukoku*  $\times$  (*Luachai*  $\times$  *Gurumatia*). The procedure was to cut the shoots down to 4-6 inches above the soil. Under the irrigated conditions in summer all the plants made good growth. After growth and flowering if any, for 2 months, the plants were again cut back. The data of number of plants flowering under these conditions is given in table 2.

It may be seen that the flowering in June-July was significantly different from that in the preceding or succeeding months. A combination of high temperature and humidity may have caused this anomalous result, but further investigations are necessary.

TABLE 1a

*Flowering ratios in F<sub>2</sub> generation of the different japonica × indica cross combination studied*

F <sub>2</sub> Cross combination	No. of insens- itive plants	No. of sensi- tive plants	Approximate ratio (fl:non-fl)	Chi <sup>2</sup> value (P=·05)	Dominant character
GAISEN MOCHI × TJAHAJA	275	18	15 : 1	0·005	Insensitivity
FUKOKU × INTAN ..	94	8	15 : 1	0·445	"
FUKOKU × Dj-MUDJAIR ..	149	11	15 : 1	0·107	"
FUKOKU × MONGCHIN ..	83	25	3 : 1	0·197	"
FUKOKU × MECANTAGO ..	48	16	3 : 1	0	"
FUKOKU × BAM. 3 ..	125	40	3 : 1	0·050	"
FUKOKU × KHAO-TA-HANG	77	31	3 : 1	0·790	"
FUKOKU × B. 405 ..	59	21	3 : 1	0·067	"
FUKOKU × MILAGROSA ..	152	43	3 : 1	0·904	"
FUKOKU × REYONG-6 ..	84	38	3 : 1	2·459	"
FUKOKU × CONCEJALA ..	78	28	3 : 1	0·113	"
FUKOKU × OTRE ..	88	32	3 : 1	0·170	"
FUKOKU × HASTIKALMI ..	84	0	(No Segregation)		
ZUIHIO × MECANTAGO ..	31	101	1 : 3	0·162	Sensitivity
ZUIHIO × B. 405 ..	39	103	1 : 3	0·460	"
ZUIHIO × OTRE ..	26	82	1 : 3	0·049	"
ZUIHIO × LUACHAI ..	6	104	1 : 15	0·119	"
ZUIHIO × REYONG-6 ..	4	74	1 : 15	0·168	"
ZUIHIO × B. 24-22 ..	14	144	1 : 15	1·838	"
ZUIHIO × MONGCHIN ..	10	144	1 : 15	0·016	"
ZUIHIO × SUBANG INTAN ..	12	141	1 : 15	0·663	"

TABLE 1b

*Flowering duration of parents*

Name of variety	Date of sowing	Date of flowering	Flowering duration
FUKOKU ..	26th March 1957	12th May 1957	48 days
ZUIHIO ..	26th March 1957	1st June 1957	68 days
GAISEN MOCHI ..	26th March 1957	4th June 1957	71 days
INDICAS ..	26th March 1957	After 1st Oct. 1957	Season bound

TABLE 2

*Flowering ratios in F<sub>2</sub> periodic ratooning experiment*

F <sub>2</sub> of Cross combination	Approximate Ratios			Total No. of plants
	April-May	June-July	Aug. Sept.	
FUKOKU × B.A.M. 9 ..	15 : 1	3 : 1	15 : 1	210
FUKOKU × (LUACHAI × GURUMATIA) ..	15 : 1	1 : 1	15 : 1	205

## DISCUSSION

The results reported refer to studies on the dominance or otherwise of insensitivity to photoperiod in *indica* × *japonica* hybrids under tropical conditions. Such a study has not been made previously and therefore the results cannot be strictly compared with previous work. Chandraratna (1955) has worked with intra-*indica* hybrids under tropical conditions and has found sensitiveness to be dominant giving a simple 3:1 ratio. Japanese workers (summarized by Morinaga, 1954) have studied genetics of photoperiod sensitivity in intra-*japonica* hybrids under temperate conditions. They have found that six pairs of genes control photoperiodic response and earliness of rice varieties, and have indicated interaction between the genes, and also the sensitiveness of two pairs of these genes to temperature in affecting the flowering duration. A parallel work by Yu and Yao (1958) using two *japonica* varieties has shown that at least two loci are concerned with the control of flowering duration. They designate the photoperiod response loci as *Se* and *se* and this is epistatic to another gene pair controlling earliness, *Fl* and *fl*. They have also shown that by suitably designing the experiment, two different ratios for earliness can be obtained from the same hybrid combination. Ramiah and Rao (1953) have cited a number of genetic studies on flowering duration in *indica* rices and have indicated the existence of multiple genes. They have also cited instances, where sensitivity was inherited as dominant and other instances where it was recessive. Environmental conditions are bound to have a profound effect on the expression of a physiological character like flowering and therefore the conditions of experiment should have a decisive effect on the results. In Cuttack, during April, May, June and July, the day-lengths are shorter than in Japan. The temperatures are, however, higher particularly in April and May. The humidity is also likely to be different from that prevailing in Japan. Since the Japanese workers have shown that temperature affects photoperiod response in rice, and since it is well established that temperature profoundly affects all aspects of plant physiology, the present results can be interpreted as revealing that temperature interacts with photoperiod in the initiation of flowering. The interpretation would be on the hypothesis that one or more loci control response to temperature in affecting flowering duration. The variety *Zuihio* is sensitive in Japan and has a very much extended duration under 13 hours or more of day-length (Morinaga and Kuriyama, 1954). However, the long day-lengths in June and July at Cuttack do not inhibit flowering in *Zuihio* and it can be termed insensitive, (but different from *Fukoku*, which is definitely insensitive) and the hybrids between *Zuihio* and the *indica* varieties behaved as sensitive. Therefore, the inference is that certain other genes concerned with temperature response, affect the expression of the genes for photoperiodic response.

The variety *Fukoku* is from Hokkaido of Northern Japan and is considered to be very sensitive to temperature conditions. On hybridization with the wild rice, *O. perennis* var. *Balunga*, the  $F_1$  hybrid behaved as photoperiod insensitive like *Fukoku*; it is significant that a character from a cultivated rice is dominant over that of a wild species. The possible explanation is that the genes modifying photoperiod response transmitted by the *Fukoku* parent cause dominance of photoperiod-insensitivity as in crosses with other cultivated rices. It may be pointed out that sensitiveness to temperature would be an important character of selective advantage in *japonica* varieties as they have to grow and yield under lower mean temperatures than in tropical countries.

## SUMMARY

The genetics of sensitivity to day-length was studied in the  $F_1$  and  $F_2$  of hybrids between the *japonica* rice varieties, *Fukoku*, *Gaisen Mochi* and *Zuihio* and a



number of *indica* varieties of rice, of different durations and photoperiod sensitivity. The data showed that the short duration and low photoperiod-sensitivity of *Fukoku* and *Gaisen Mochi* were dominant over the long duration and high photoperiod-sensitivity of the *indica* parents and of a wild rice studied, giving  $F_2$  ratios of 15 : 1 and 3 : 1. The corresponding *Zuihio* hybrids showed sensitivity and in the  $F_2$  insensitivity occurred as a recessive character in ratios of 1 : 3 and 1 : 15. The variety *Zuihio*, which is recorded in Japan to be sensitive to photoperiods, behaved almost as an insensitive variety at Cuttack. It is inferred that temperature, or some other environmental factor, affects the expression of photoperiod response and the present results were interpreted by assuming that the genes modifying photoperiod response showed segregation in the hybrids studied.

#### ACKNOWLEDGEMENTS

The authors are indebted to the Director, Central Rice Research Institute, Cuttack for facilities and encouragement. This work was started during a project for breeding *japonica*  $\times$  *indica* hybrids, sponsored by the Food and Agriculture Organization of United Nations.

#### REFERENCES

- Chandraratna, M. F. (1955). Genetics of photoperiod sensitivity in rice. *J. Genet.*, **53**: 215-23.  
Morinaga, T. (1954). Studies on the photoperiodism in rice (Abstracts of Japanese Literature). *Reports for the fifth meeting of the I.R.C. Working Party on Rice Breeding, Tokyo*: 21-34.  
——— and Kuriyama, H. (1954). Some experiments on the photoperiodism in rice. *Reports for the fifth meeting of the Working Party on Rice Breeding, Tokyo*: 35-63.  
Ramiah, K. and Rao, M. B. V. N. (1953). *Rice Breeding and Genetics*. I.C.A.R. Scientific Monograph No. 19, New Delhi.  
Yu, C. J. and Yao, Y. T. (1958). Über die Vererbung der Ausschusszeiten beim Reis. *Jap. J. Genet.*, **32**: 179-88.

# CYTOGENETICAL EFFECTS OF X-RAYS, THERMAL NEUTRONS AND $\beta$ -PARTICLES ON *ORYZA SATIVA* L.

S. V. S. SHASTRY and K. RAMAIAH

*Division of Botany, Indian Agricultural Research Institute, New Delhi-12*

MUTATION studies in rice, *Oryza sativa* were initiated by Ichijima (1934) in Japan and Ramiah and Parthasarathy (1936) in India. The mutants secured in their studies were chlorophyll deficient or teratological abnormalities which have not roused much interest among plant breeders. More recently, however, workers in U.S.A. (Beachell, 1957), China (Chang, 1959), Japan (Masima and Kawai, 1958) and India (Bora and Rao, 1958) reported different viable mutants which might serve as useful breeding material for the improvement of this crop. The present study was undertaken to determine the morphological and cytogenetic changes accompanying radiation with three mutagens, and to determine whether the mutation spectrum can be altered by employing specific mutagens.

## MATERIALS AND METHODS

A strain of rice, N.P. 130 (bred at the I.A.R.I.), was chosen for this study. Dry and soaked, dehusked seeds, spread in a single layer in petri dishes, were subjected to X-irradiation employing a Philips medical X-ray unit. Irradiation with thermal neutrons was done at the "Apsara" reactor through the courtesy of the Atomic Energy Establishment, Trombay. For Beta irradiation, dehusked seeds of rice were soaked in dilute solution of  $H_2S^{35}O_4$  received from Harvell in the U.K.

Emergence of coleoptile was taken as indication of germination. Lethality of the treatment was determined at various time intervals, but data at the 14th day alone are used in the discussion of the results. The uptake of  $S^{35}$  by the seeds was confirmed by autoradiography of the seedlings.

Spikes of suitable stage were fixed in acetic alcohol (1 : 3 by volume) to which traces of ferric chloride were added. After fixation at 14°C for 24 to 48 hours, the material was transferred to 70 per cent. ethyl alcohol in which it was stored till used. The anthers were squashed in 1 per cent. aceto-carmin to which traces of ferric acetate were added.

For the study of mutations, the  $M_2$  generation was raised as ear-row progenies from the selfed tillers of the  $M_1$  plants.

## RESULTS

**Germination.**—Germination was completely unaffected even at the highest dose of X-rays (44 kr. to soaked seeds) employed, while it was reduced only by 12 per cent. in the highest dose of (9  $\mu$ c per seed)  $S^{35}$  treatment. Germination was significantly quicker in all the doses of thermal neutron irradiation. While the control exhibited germination of only 36.66 per cent. of seeds at 24 hours, at an integral flux of  $3.29 \times 10^{12}$  of thermal neutrons, 90.24 per cent. of the seed germinated by this time.

**Lethality.**—Lethality of the seedlings following irradiation was pronounced in X-ray and  $S^{35}$  treatments while it was negligible in the treatment with thermal neutrons. Data on lethality are presented in table 1. The L.D. 50 for the soaked series was below 11 kr, while for dry seed it was between 22 and 33 kr, for this variety. 3, 6 and 9  $\mu$ c of  $S^{35}$ /seed were lethal to 29.0, 60.0 and 75.0 per cent. of the seedlings.

Lethality following irradiation with thermal neutrons was negligible and was comparable to that in the control series.

TABLE 1

*Lethality in  $M_1$  generation of rice treated with X-rays, thermal neutrons and  $\beta$ -particles*

Treatment	Dose	Number of seeds treated	Percentage lethality on 14th day	Percentage increase over control
X-rays (dry) seeds	.. 11 kr	110	30.9	24.8
	22 kr	106	38.7	32.6
	33 kr	110	74.5	68.4
	44 kr	108	97.2	91.1
X-rays (soaked) seeds	.. 11 kr	96	95.8	89.7
	22 kr	96	100.0	93.9
	33 kr	97	100.0	93.9
	44 kr	94	100.0	93.9
Thermal neutrons	.. $3.29 \times 10^{12}$	206	21.9	0.0
	$4.32 \times 10^{12}$	248	36.3	4.6
	$4.40 \times 10^{12}$	250	30.4	0.0
$\beta$ -particles	.. 3 $\mu$ c per seed	100	29.0	23.0
	6 $\mu$ c per seed	100	60.0	54.0
	9 $\mu$ c per seed	100	75.0	69.0

*Height.*—Irradiation with X-rays markedly reduced the height of the seedlings, this reduction being very pronounced beyond 22 kr in the dry and 11 kr in the soaked treatments. Some of the seedlings in these treatments were broad-leaved, exceedingly short and exhibited premature tillering. Likewise, the seedlings originating from the seed treated with 9  $\mu$ c of  $S^{35}$  per seed were significantly shorter compared to the control and lower doses of isotope treatment. Irradiation with thermal neutrons in the dosage range tried in the present study, however, led to an increase in height (21.1-29.6 per cent.), as against the control, at 7 days. Height reduction following neutron irradiation was only 1.2 to 8.5 per cent. at the 14th day while it was 3.7-80.3 per cent. following X-irradiation. Further, the coefficient of variability for height within the treatments of X-rays ranged from 13.42 to 34.0 at 7 days and 41.6 to 61.5 at 14 days, while those in the neutron irradiation treatments ranged from 23.0 to 30.5 at 7 days and 28.2-30.4 at 14 days. It would be clear that the height of the seedlings at the 14th day was more uniform following neutron irradiation than under X-irradiation.

*Chimeras.*—Following X-ray and thermal neutron irradiation, five plants were green-*albina striatas*, and one was a complex chimera with green-*albina-xantha* stripes on different tillers. Except for one green-*albina striata* which segregated for green and *albina* plants, all the others gave normal green plants in  $M_2$  generation. Further, none of these exhibited any detectable cytological abnormalities in the  $M_1$  generation,



*Meiosis*.—Cytological study of the irradiated plants was confined only to meiosis since the available techniques do not permit quantitative study of chromosome aberrations in somatic metaphases.

Multivalents were of most frequent occurrence following X-irradiation. The highest association observed was a hexavalent (Fig. 3), while the number of quadrivalents ranged from 1-3 per PMC (Figs. 2, 5 and 6). Meiotic abnormalities occurred in a small percentage of the cells studied, not only in the treatment as a whole, but also within the single ear of the  $M_1$  plant. In some  $M_1$  plants, the quadrivalents were asymmetrical. Following thermal neutron irradiation, quadrivalents were observed in 5 out of 98 PMCs studied in only one out of the seven plants that were treated at a dosage of  $3.5 \times 10^{17}$  integral flux. In other treatments no abnormalities were recorded. A single quadrivalent per PMC was recorded in 2 out of 15 plants studied in the treatment, 9  $\mu$ c of  $S^{35}$  per seed.

Chromosomal bridges accompanied by fragments (Fig. 4) were less frequent than multivalents in all the treatments studied. These were recorded only in 2 out of 18 and 1 out of 17 plants studied in isotope treated and X-irradiated material respectively and even in these their frequency was low in a single ear of the  $M_1$  plant. Unequal bivalents at diplotene, indicative of terminal deletion (Fig. 1) of one of the chromosomes of the bivalent, were recovered in isotope treated material, but not in material treated with other mutagens. Minutes at diplotene were recorded in a few PMCs in all the treatments. Pachytene analysis revealed small differential segments (Fig. 7) in all the treatments. A summary of the meiotic data of the irradiated plants is presented in table 2.

TABLE 2

*Meiotic abnormalities in  $M_1$  generation of rice treated with X-rays and  $\beta$ -particles*

Treatment	Dose	No. of plants studied	No. of PMCs studied	Multivalent frequencies				Chromatin bridges	Differential segments	Unequal bivalents	Univalents	Minutes
				1 <sub>IV</sub>	2 <sub>IV</sub>	3 <sub>IV</sub>	1 <sub>VI</sub>					
X-rays (dry seeds)	22 kr.	11	348	51	6	..	6	1	1	..	..	..
	33 kr.	5	228	65	5	2	..	..	1	..	..	..
	44 kr.	1	33	13	..	..	..	..	..	..	..	..
$\beta$ -particles( $S^{35}$ )	6 $\mu$ c	3	65	..	..	..	..	..	..	..	..	3
	9 $\mu$ c	15	591	14	4	..	..	7	..	4	2	6

*Mutations*.—Quantitative data on mutation rate were collected only for chlorophyll mutations in  $M_2$  generation (Table 3). The mature plants also exhibited considerable variability for awns, flowering duration, tillering and height, some plants being strikingly different from the controls. However, their breeding behaviour would have to be confirmed before they are considered as mutations.

Chlorophyll mutation rate exhibited a steady increase with an increase in dosage of isotope treatment while it declined with the increase in dosage of X-rays, the exception being of 44 kr treatment where the number of plants studied itself was limited

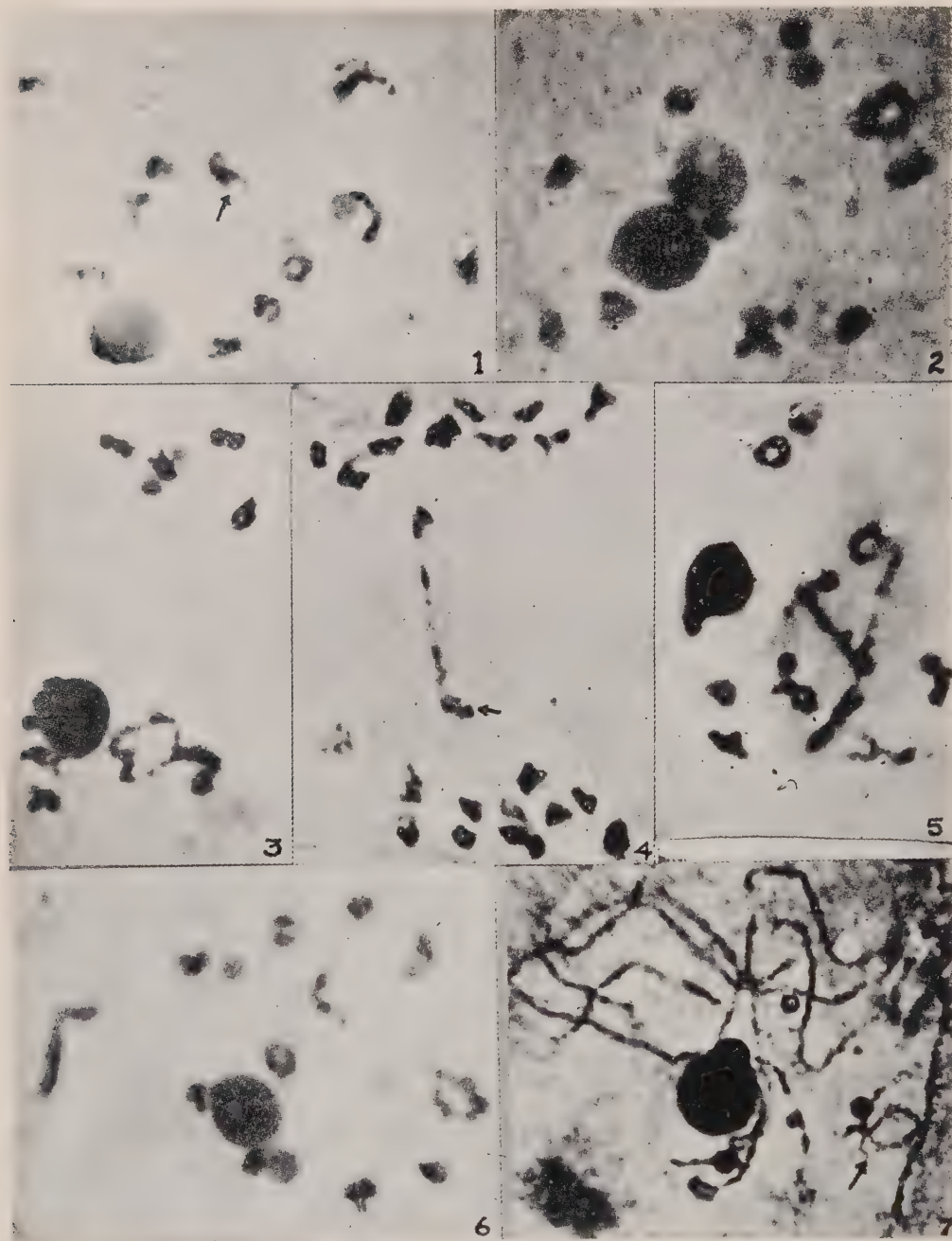


FIG. 1. S35 treatment, 9  $\mu$ c per seed. Diplotene 12<sub>II</sub>. One bivalent ( $\rightarrow$ ) unequal.  
 FIG. 2. X-rays, 33 kr. Diakinesis. 1<sub>IV</sub> + 10<sub>IV</sub>. Two large nucleoli.  
 FIG. 3. X-rays, 22 kr. Diakinesis. 1<sub>VI</sub> + 9<sub>II</sub>. Two small nucleoli.  
 FIG. 4. S35 treatment, 9  $\mu$ c per seed. Anaphase I. Chromatin bridge with a fragment ( $\rightarrow$ ).  
 FIG. 5. X-rays, 22 kr. Diplotene. 1<sub>IV</sub> + 10<sub>II</sub>.  
 FIG. 6. X-rays, 33 kr. Diakinesis. 1<sub>IV</sub> + 10<sub>II</sub>. One large and one small nucleolus.  
 FIG. 7. X-rays, 22 kr. Pachytene. Differential segment ( $\rightarrow$ ) on one bivalent.

by reason of poor viability. The chlorophyll mutation rate in relation to different doses of neutron irradiation was not conclusive. Further, of the 15 segregating cultures in all the treatments, only 7 exhibited a clear 3 : 1 ratio of normal : mutants while the rest were characterised by a great shortage of mutant phenotypes.

TABLE 3

*Frequency of chlorophyll mutations in  $M_2$  generation of rice treated with X-rays, thermal neutrons and  $\beta$ -particles*

Treatment	Dose	No. of plants studied	Percentage of $M_1$ plants segregating for		Percentage of total chlorophyll mutations
			<i>albina</i>	<i>xantha</i>	
X-rays (dry seeds)	.. 11 kr	40	7.5	2.5	10.0
	22 kr	49	2.0	4.1	6.1
	33 kr	8	..	..	0.0
	44 kr	2	50.0	..	50.0
Thermal neutrons	.. $3.29 \times 10^{12}$	60	1.7	..	1.7
	$4.32 \times 10^{12}$	10	..	10.0	10.0
	$4.40 \times 10^{12}$	12	..	..	0.0
$\beta$ -particles ( $S^{35}$ )	.. 3 $\mu$ c per seed	5	..	..	0.0
	6 $\mu$ c per seed	5	..	20.0	20.0
	9 $\mu$ c per seed	7	14.3	42.9	57.2

## DISCUSSION

*Chromosome breakage.*—Cytological and genetic effects of ionizing radiations are traceable largely to chromosome breakage at the microscopic and sub-microscopic levels. Irrespective of the mechanism of their production (direct or indirect effects), the breaks might undergo restitution or reunion or remain open. While an accurate estimation of the breakage frequencies is possible only at the earliest intervals after irradiation, the genetic effects of these treatments are more clearly visualized by the studies of meiosis of the  $M_1$  plants.

Multivalents were the most frequent abnormality noted in the  $M_1$  generation, the highest association observed being a hexavalent. These were most frequent in X-rayed material, followed by neutron and isotope treated ones. The low recovery of multivalents after neutron treatment might be due to the low dosage range employed, as evidenced by the stimulation of growth noted in the present study and by comparison with the dosage employed by Bora and Rao (1958). The low recovery of multivalents in isotope-treated material is more likely to be due to the low probability of origin of two breaks in the same nucleus following chronic internal radiation. Following X-irradiation, however, several breaks are likely to be produced in the same cell simultaneously, some of which might undergo reunion. Ichijima (1934), Parthasarathy (1938), Oka *et al.* (1953), Ouang (1958), Soriano (1959) and others reported quadrivalents following X-irradiation.

*Chimeric nature of  $M_1$  plants.*—The mature seeds of *Oryza sativa* have 2-3 primordia laid down at maturity (Kepling, 1940). When such seeds are irradiated it is possible



that only one of the primordia is affected cytologically. In such a case only one of the major tillers may exhibit cytological abnormalities and genetic changes. This situation is realized in most of the cereals (Mackey, 1954). Even in dicotyledonous plants, only single branches of  $M_1$  plants exhibit chromosome abnormalities and results in mutations (Blixt, Ehrenberg, and Gelin, 1958; and Gottschalk, 1960). The remaining tillers or branches might originate either from the mutant sector or from the normal tissue. The present study, where the individual tillers were separately raised in  $M_2$  generation, clearly revealed that only 1-3 tillers per plant exhibit chlorophyll mutants. Exceptionally, however, all the tillers (seven) of one  $M_1$  plant exhibited mutations (Achari, unpublished).

The genetical and cytological identity of the cells of a single tiller itself is not universal and is dependent upon the number of cells in the primordium which give rise to it. In barley, it was at one time assumed that a single cell in the primordium gives rise to a tiller by a series of mitotic divisions, since Caldecott and Smith (1952) found that all PMCs of a spike had identical chromosome aberrations. Mackey (1954), on the other hand, recovered chimeras for panicle type in the same ear, thereby indicating that it is possible for more than one cell in the primordium to contribute to the formation of the tiller. Anderson, Longley, Li and Retherford, (1949) likewise, showed that within a single tassel of maize, the chromosome abnormalities differed in the different branches and they inferred that more than one cell of the primordium is involved in the formation of the tassel.

The low frequency with which the chromosomal aberrations were recovered in X-irradiated rice might be considered in the light of the above discussion. The growing points of rice are perhaps so organized that more than 2-3 cells might contribute to the formation of a single panicle. In such a case, following X-irradiation, even within the same tiller, the chromosome aberrations might cover a broad spectrum depending upon the relative damage to the different cells in the primordium.

Isotope treated material can be expected to be highly complex chimera for yet another reason.  $\beta$ -particles are emitted at different intervals of time, with every ionization produced by the radioactive decay leading to a new cytogenetic event, with howsoever low a probability. In such cases, the operation of diplontic selection (Gaul, 1959) and the origin of fresh breaks proceed simultaneously during the entire growth phase so long as the activity lasts. In the short-duration variety used in the present study, by the time  $M_1$  plants are undergoing meiosis, even the half-life of the isotope ( $S^{35}$ , 87.1 days) is not passed. Some of the terminal deletions recorded might owe their origin to chromosome breakage one or two divisions prior to the formation of PMCs. In such a case the aberrant cells are expected to be limited in number as was realized in the present study. Superimposed upon these limitations are the smallness of the chromosomes and the high terminalization coefficient in rice leading to the reduction in the associations and thereby increasing the variability within the same panicle.

*Diplontic selection.*—It is commonly observed that following X-irradiation, the chromosomal aberrations are the highest at the earliest interval and show a decline in samples taken at 48-96 hours after irradiation (Bhaskaran and Swaminathan, 1960). These observations are indicative of "threshold effects" in the detection of chromosome abnormalities. At very low doses, the frequency of cytogenetical changes in a tissue is less and these might get further reduced by lethality of the affected cells. At very high doses, the severely damaged cells might be eliminated by lethality followed by proliferation of normal tissue. It is only at a "critical dose" that the frequency of occurrence of abnormalities is considerably greater compared to the elimination of such abnormalities. In the X-rayed material in the present study, the operation of diplontic selection was clearly noticeable. At very low doses, 11 and 22 kr, seedling lethality was less and chromosomal abnormalities were more frequent than at high

doses (33 and 44 kr. dry and 11 to 44 kr. soaked) where the lethality was great and the abnormalities recorded at meiosis were considerably less. This observation is most readily interpreted as being due to the operation of rigorous selection against the aberrant cells at higher doses.

*Chlorophyll mutations.*—Chlorophyll mutations are very commonly encountered on irradiation of diploid cereals. While these occur with a very low frequency (1 in 500 to 1,000) even in untreated populations of some varieties of rice (Imai, 1935; Ramiah, 1953), those originating from irradiation are unmistakable by their occurrence in  $M_2$  generation in approximately a 3 : 1 ratio of normal to mutants. The chlorophyll mutations reported in the present study were of two types—*albina* which were fully white and *xantha* which were fully yellow. While both were lethal, the latter died much earlier. Similar differences have been noted in the survival of the mutants in wheat (Gustafsson, 1947).

Ramiah and Parthasarathy (1938) reported the segregation of 3 : 1 and 15 : 1 of normal : *albina* and of 3 : 1 segregation for normal : *xantha* in X-rayed material of rice. Kadam (1941), however, reported the ratios 15 : 1 and 3 : 1 for green : *xantha* in X-rayed material of rice. At the time the investigations were undertaken by the above mentioned authors, the necessity of keeping the different tillers of the  $M_1$  plants separately was not realized. Consequently, these results are not strictly comparable with those of the present investigation where the ear-row progenies were raised separately. However, a segregation of 15 : 1 necessitates a simultaneous mutation in 2 loci controlling the same character which can happen, only at a very low probability. The results obtained by Ramiah and Parthasarathy (1938) and Kadam (1941) might well be taken as an indication of a mutation at a single locus but the great shortage of the mutant class might be due to bulking of affected and unaffected tillers.

The results obtained in the present investigation may be examined in the light of the above discussion. Barring the 44 kr treatment, where the population was limited to two  $M_1$  plants, in all other treatments chlorophyll mutations occurred only in 1.7 to 57.2 per cent of the  $M_1$  plants studied. Of these again, more than 50 per cent of the cultures exhibited significant deviation from a 3 : 1 ratio even though the tillers were scored separately. In general, the mutant types were in considerable shortage. While some of these can fit into 15 : 1 or 63 : 1 ratios, such an attempt was not made in the interpretation of the data since the occurrence of simultaneous mutation in 2 or 3 loci governing the same character is a highly remote possibility. On the other hand, if it is postulated that a single tiller of the  $M_1$  plant itself is a chimera since it originates from more than one cell of the primordium, a conclusion adequately supported by the cytological studies presented here, the deficiency of the mutant types can be easily understood. Bekendam (1960) arrived at a similar conclusion based upon the studies of genetic ratios in irradiated rice. Further, some of the mutants might be associated with gross structural changes which might reduce their transmission in the haplontic phase. Even in the diplontic phase, associated with homozygosity for some of these mutants, embryonic elimination (diplontic sterility) might be operating or the seeds which are to give rise to *albina* and *xantha* phenotypes might exhibit poor germination. Unfortunately, in the present study, the sterility of the  $M_1$  plants was not studied and hence some of these alternatives could not be eliminated.

The next significant observation of the present study was the negative relationship observed between dosage of X-rays and the rate of chlorophyll mutations. Although the number of plants studied in the different treatments was different (for reasons of viability), this general tendency was obvious. Following neutron treatment, however, the relationship was conflicting. The chlorophyll mutation rate in  $S^{35}$  treatment, in sharp contrast to that of other two mutagens employed, exhibited a steady increase with the increase of activity. However, dosimetry with regard to isotope treatment is difficult since the absorption of the isotope can vary and, further, these



are cumulative radiations. On the basis of these data, it is possible to draw some general conclusions. Irradiation with X-rays might lead to considerable physiological damage and therefore might lead to elimination of drastically affected cells in the surviving seedlings by diplontic selection. This would result in a drop in chromosomal changes and chlorophyll mutation rate with increase in dosages. Following neutron irradiation, however, the nuclear damage is considerable while the physiological change is less (Ehrenberg, 1955), as was evidenced by the lethality data in the present study. Consequently, it is expected that chlorophyll mutation rate would increase with the increase of dosage. The data secured in the present study, however, did not support such expectation. It was perhaps because the dosage range tried was by itself low; this aspect needs verification in further experiments. The increased chlorophyll mutation rate (57.2 per cent) at a dose of 9  $\mu$ c of  $S^{35}$  per seed, which is lethal to 75 per cent of the seedlings, clearly indicates that the cumulative effects of the radiations might offer a positive approach to maximisation of mutation rates and that even doses beyond 9  $\mu$ c per seed might be more effective in producing chlorophyll mutations. Higher lethality in such treatments can be partly offset by taking large number of seeds per treatment. This also points to the possibility that lethality and genetic damage are controlled by two different phenomena.

Although it is realized that, by and large, mutational events following ionizing radiations occur at random with reference to nuclear targets and the evidence in favour of preferential breakage following ionizing radiations is limited (Swaminathan and Natarajan, 1957), the spectrum of mutation is greatly influenced by the mutagen employed. In barley, the *erectoides* mutations occurred more frequently following neutron irradiation, while the *speltoides* mutations occurred more frequently following X-irradiation (Mackey, 1954; Natarajan, Sikka and Swaminathan, 1958). The present study indicates that the *xantha* mutants were more common in the isotope treated material than in the X-rayed or thermal neutron treated ones. This observation, however, requires confirmation in further experiments since the number of  $M_1$  plants studied was limited.

#### SUMMARY

A variety of rice, N.P. 130, was irradiated with X-rays, thermal neutrons and  $\beta$ -particles from  $S^{35}$ . Data on germination, lethality, height and meiosis of the  $M_1$  generation are discussed. The chimeric nature of  $M_1$  plants and its significance for the yield of chromosomal aberrations in  $M_1$  generation and the recovery of mutations in  $M_2$  generation are discussed. Data on chlorophyll mutation indicated that *xantha* mutations were more frequently encountered following treatment with  $S^{35}$  while *albinas* were more frequent following X-irradiation.

#### ACKNOWLEDGEMENTS

We express our gratitude to Dr. B. P. Pal, Director and Dr. A. B. Joshi, Head of the Division of Botany, for their interest in the study and to Dr. M. S. Swaminathan and Dr. S. Bhaskaran for valuable discussions. One of us (K. Ramaiah) is grateful to the Department of Agriculture, Government of Andhra Pradesh for deputing him to the Indian Agricultural Research Institute, New Delhi for post-graduate training.

#### REFERENCES

- Anderson, E., Longley, A. E., Li, C. H. and Retherford, K. L. (1949). Hereditary effects produced in maize by radiations from the Bikini atomic bomb. I. Studies on seedlings and pollen of the exposed generation. *Genetics*, **34**: 639-46.



- Beachel, H. M. (1957). The use of X-rays and thermal neutrons in producing mutations in rice. *I.R.C. News Letter*, **6**: 18-22.
- Bekendam, J. (1960). Note in *Symposia on the effects of ionizing radiations on seeds and their significance for crop improvement*. Karlsruhe.
- Bhaskaran, S. and Swaminathan, M. S. (1960). Polyploidy and radio sensitivity in wheat and barley. I. Cytological and Cytochemical studies (In press).
- Blixt, S., Ehrenberg, L. and Gelin, O. E. V. (1958). Quantitative studies of induced mutation in peas. I. Methodological investigation. *Agri. Horti. Genetica*, **16**: 238-49.
- Bora, K. C. and Rao, N. S. (1958). Experience with rice (*Oryza sativa*) on the induction of mutation. *Proc. 2nd Intern. Conf. on Peaceful uses of Atomic Energy*, **27**: 306-13.
- Caldecott, R. S. and Smith, L. (1952). A study of X-ray induced chromosomal aberration in barley. *Cytologia*, **17**: 224-42.
- Chang, H. S. (1959). Application of irradiation treatment for induced mutants. *I.R.C. News Letter*, **8**: 1-7.
- Ehrenberg, L. (1955). The radiation induced growth inhibition. *Botaniska, Nohser*, **108**(2): 184-215.
- (1955). Factors influencing radiation induced lethality, sterility and mutation in barley. *Hereditas, Lund*, **41**: 123-46.
- Gaul, H. (1959). Über die cheimarenbildung in Gerstenpflanzen nach Röntgenbestrahlung von Samen. (Chimera formation in barley plants after X-irradiation of seed). *Flora, Jena*, **147**: 207-41.
- Gustafsson, A. (1947). Mutations in Agricultural Plants. *Hereditas, Lund*, **33**: 1-100.
- Imai, Y. (1935). The effect of X-rays on the production of sterile rice. *Jap. J. Genet.*, **10**: 233-41.
- Ichijima, K. (1934). On the artificial induced mutation and polyploid plants of rice occurring in subsequent generations. *Proc. Imp. Acad. Tokyo*, **10**: 381-91.
- Kadam, B. S. (1941). Genic analysis of rice. II. Chlorophyll deficiency. *Indian J. Genet.*, **1**: 13-26.
- Kepling, L.C.P. (1940). Cited by Bekendam, (1960).
- Mackey, J. (1954). Mutation breeding in polyploid cereals. *Acta Agri. Scand.*, **4**: 549-57.
- (1954). Neutrons and X-ray experiments in wheat and a revision of the speltoid problem. *Hereditas, Lund*, **40**: 65-180.
- Masima, T. and Kawai, T. (1958). Mutations of rice induced by Radiosotope P<sup>32</sup>. *Proc. 2nd Inter. Conf. Peaceful uses of Atomic Energy*, **27**: 293-98.
- Natarajan, A. T., Sikka, S. M. and Swaminathan, M. S. (1958). Polyploidy, Radiation sensitivity and mutation frequency in wheats. *Proc. 2nd Inter. Conf. Peaceful uses of Atomic Energy*, **27**: 321-31.
- Ouang (Wang), T. Y. (1958). Mutations induced by X-rays in cultivated rice (*O. sativa* L.). *J. Agri. Trop. Bot. Appl.*, **5**: 681-90.
- Oka, H. I., Chang, T. T. and Pong, M. S. (1953). Reciprocal translocation in rice. *Jap. J. Genet.*, **4**: 49-54.
- Parthasarathy, N. (1938). Cytogenetical studies in Oryzae and Phalarideae. Cytogenetics of some X-ray derivatives in rice (*Oryza sativa*, L.). *J. Genet.*, **37**: 1-40.
- Ramiah, K. (1953). *Rice Breeding and Genetics*. I.C.A.R. Science Monograph, No. 19, New Delhi.
- and Parthasarathy, N. (1936). An ageotropic mutation in X-rayed rice. *Curr. Sci.*, **5**: 135-36.
- Shastri, S. V. S., Ranga Rao, D. R. and Misra, R. N. (1960). Pachytene analysis in Oryza. I. Chromosome morphology in *Oryza Sativa*. *Indian J. Genet.*, **20**: 15-21.
- Soriano, J. D. (1959). X-ray induced reciprocal translocations and chlorophyll mutations in rice. *Bot. Gaz.*, **120**: 162-65.

## "XENIA" IN OLEIFEROUS BRASSICAE

S. S. RAJAN and S. B. P. RAO

*Division of Botany, Indian Agricultural Research Institute, New Delhi-12.*

WHEN plants of *Brassica chinensis* were crossed as females with different types of *toria*, a differential increase in the size of the pods and of the seeds has been reported (Singh, 1957). This has been explained as being due to the phenomenon called by the author "Xenia", and a suggestion has been made that this phenomenon can be usefully exploited in increasing the seed yield of self-incompatible species of *Brassica*. It would appear that what the author implies here by the term "xenia" is the phenomenon generally referred to as 'metaxenia'. The basic issues involved are (i) whether increase in seed size is to be termed as a xenia effect, particularly when the bulk (over 98 per cent) of the weight of the seed is made up of cotyledons; (ii) whether the reported increase in yield is due to an increase in seed weight or in seed number; (iii) whether the increase in siliqua size (presumably length) is the cause or the effect of increase in seed weight or number.

The present study was undertaken to find out whether similar observations could be repeated in *toria*. The method of analysis attempted here is to find out whether, under a wide spectrum of pollination provided by varying degrees of random to assortative matings, a given group of females show any relationship between seed number, fruit size and seed weight. Metaxenia effect, if present, should be manifest as correlations, between any two of these characters, widely differing in sign and magnitude.

### MATERIALS AND METHODS

The experimental material used was colchicine-induced autotetraploid stocks of *toria*, *Brassica campestris* var. *toria*, in the  $C_{18}$  generation and the diploid Type 22. The material was divided into five different sets as follows:

(i) *Set I*.—From a general, non-experimental field of tetraploid *toria*, fifty plants were chosen at random to serve as females. The mating was completely random, without selfing on account of self incompatibility of this material. This set is referred to as 'uncontrolled pollinated set'.

(ii) *Set II*.—This set consisted of fifty plants sampled from a 'polycross field' made up of open pollinated progenies of plants selected on their performance in the previous season. Two specific features of this set were (a) the females were from progenies of selected plants and (b) all the females had the maximum opportunity to be fertilized by all the males. This set is referred to as 'Polycross set'.

(iii) *Set III*.—Open pollinated progenies of six of the selections included in the polycross field were raised in pots (minimum of three pots each) in a net house far away from any other *Brassica* plant. Pollination was through the agency of bees but was confined to *inter se* crossing of 27 plants. This set is similar to Set II except in that, all combinations are not expected due to reduced randomization and replications. On the other hand, all matings are necessarily *inter se* through the male parent cannot be specified in each case. This is referred to as 'Restricted pollinated set'.

(iv) *Set IV*.—Five of the six selections referred to in Set III were used as females using in each case three different males. The pollination was done by hand under controlled conditions, (though emasculation was omitted on account of self incompatibility). This differs from all the other sets in that both the parents of each

pollination are known. Omitting reciprocals, 17 different cross combinations amongst five selections were made. This set is referred to as 'Controlled pollinated set'.

(v) *Set V*.—This set was similar to Set I above except that the material was diploid *toria* type 22 and was intended to serve as a check to indicate whether the trends of observation in the other four sets are comparable to that in the diploids, or are peculiar to the tetraploids as a consequence of tetraploid genetics and physiology.

It will be seen that in the four sets described above, from Set I, in which the females had no selection history and males were unknown, to Set IV, in which selected females were mated to specific males complete by random to assortative mating is obtained.

In all the five sets, observations were recorded on seed fertility, expressed as the number of seeds per siliqua, and fruit size, expressed as the length of the seed-bearing part of the siliquae, *i.e.*, excluding the beak and the pedicel, at the mature stage. Seed weights were recorded on 100 seeds in sets III and IV. Sampling of fruits was done from the middle third of the main stem from which ten fruits were picked at random, a procedure found to be representative of the entire plant and routine in these laboratories. Ovules were counted by dissection of ovaries collected on the day of flower opening. Data on seed number, fruit size and seed weight were collected at the mature stage.

Coefficients of correlations were worked out in the usual manner and their significance tested by the 't' test and also after 'z' transformation.

#### RESULTS

Table 1 records the number of seeds per siliqua and the siliqua length (seed bearing portion) and the correlation coefficients between them in the different sets under observation. The data from the controlled pollinated set is presented female-parent-wise as well as collectively. It will be seen from the table that there is a significant positive correlation between seed number and siliqua size under the different types of pollinations. Only in two cases, *viz.* in female parent IX and XI, are the correlations not significant. In the former it misses being significant rather narrowly as will be seen from the 't' value in table 1. The different 'r' values do not differ amongst themselves significantly, as comparison after 'z' transformation shows, except in the case of female parents XI and V. The pooled r values of the diploids, of the tetraploids in all the four sets, and of all the females of set IV, shown in table 2, indicate that the correlation, in its magnitude and sign, is uniform over all the different degrees of assortative pollination. From this we can derive the following conclusions (i) the siliqua length is positively correlated with seed number, the 'r' value being 0.4, (ii) this correlation is not disturbed by varying the randomness (or assortativeness) of the male parents, nor is it disturbed by autopolyploidy.

From the foregoing it appears that the size of the siliqua is determined by the seed number. This, in turn, is determined by the number of ovules and by the proportion of these ovules that are fertilized and develop into mature seed. This is clearly shown by the data in table 3 in which the correlation between the ovule number on the day of opening of the flower and the seed number at maturity is presented. Thirty plants each of diploids and tetraploids were sampled at random and five ovaries from each plant from the middle of the main stem were fixed in acetic alcohol on the day of the opening of the flower for this purpose. Ovule counts were made under a dissecting microscope. From the same plants seed fertility counts were made at the mature stage from the siliquae on the main stem. The data were compared and correlations worked out. It is seen that both in the tetraploids and in the diploids there is a highly significant, positive correlation between the two characters. This suggests that the differences in the seed fertility amongst the plants in the tetraploids as well as in the



TABLE 1

*The number of seeds per siliqua and siliqua length and the correlation between them under different conditions of pollination*

Sl. No.	Condition of Pollination	Total number of plants studied	Number of seeds per siliqua		Size of fruit in mm.		Correlation between seed number & fruit size		Unit fruit length per seed in mm.
			Mean	Standard deviation	Mean	Standard deviation	'r' value	't' value	
1.	Uncontrolled pollination	368	16.03	4.82	43.4	2.98	+0.366*	24.73	2.707
2.	Polycross set ..	495	13.80	6.01	44.6	5.03	+0.44*	24.9	3.231
3.	Restricted Pollination	270	11.8	4.8	42.95	6.2	+0.44*	8.08	3.639
4.	Controlled Pollination (females pooled) ..	180	14.07	4.6	45.77	6.8	+0.486*	7.0	3.253
5.	Controlled Pollination								
	i. ♀VI × ♂XI, III, IX	30	14.2	3.57	46.96	9.27	+0.35*	2.0	3.308
	ii. ♀V × ♂VI, XI, III	30	10.1	4.58	41.1	6.33	+0.65*	4.5	4.069
	iii. ♀III × ♂IX, V, VI, XI	40	17.5	2.67	46.77	6.31	+0.50*	3.06	2.672
	iv. ♀XI × ♂V, IX, VI	30	13.8	5.89	48.90	7.14	+0.19	1.1	3.543
	v. ♀IX × ♂V, VI, III, XI	40	14.15	4.47	46.57	4.32	+0.24	1.75	3.291
6.	Uncontrolled Pollination (diploid) ..	240	14.1	4.79	43.8	13.8	+0.359*	6.09	3.106

\*Significant at 5% level.

TABLE 2

*Pooled estimates of correlation coefficients between seed number per siliqua and siliqua length in the different sets*

Sl. No.	Material	Pooled estimate of 'r'
1.	Females of set IV only ..	0.397
2.	Females of sets I, II, III & IV ..	0.42
3.	Females of set V only ..	0.37
4.	Females of sets I, II, III, IV & V ..	0.41

TABLE 3

*Correlation coefficient between ovule number per ovary on the day of flower opening and seed number per siliqua at maturity*

Sl. No.	Material	Value of 'r'	Value of 't'
1.	Tetraploid <i>toria</i> (general) ..	0.91**	5.7
2.	Diploid <i>toria</i> (general) ..	0.97**	6.1

\*\*Significant @ 1 per cent.

diploids are due differences in ovule numbers inherent in the females and not due to differences in the number of ovules that are fertilized and developed to mature seeds.

The relationship of seed weight with siliqua size and seed number is indicated by the correlations given in table 4. Under total assortative pollination as obtained in the controlled pollinated set, a high positive correlation between seed number and seed weight exists which is significant at 1 per cent. level. Siliqua size, on the other hand, shows no correlation with seed weight. Under random mating, as obtained in the restricted pollinated set, no relationship is significant. It has already been shown that seed number and ovule number are positively highly correlated. Considering the fact that ovule number is determined ontogenically much earlier than flowering, we may conclude that seed weight shows a variation independent of the male parent particularly since it shows variation dependent on seed fertility.

TABLE 4

*The relationship between seed fertility, fruit size and seed weight in controlled pollinated and restricted pollinated sets*

Material	Correlation between seed fertility and seed weight		Correlation between fruit size and seed weight		Mean seed fertility	Mean fruit size in mm.	Mean 100 seed weight in gm.
	'r' value	't' value	'r' value	't' value			
1. Females from the controlled pollinated set ..	0.7**	3.74	-0.01	0.98 n.s.	14.51 ±0.9357	46.343 ±0.56	0.47418 ±0.02283
2. Females from the restricted pollinated set ..	-0.44	0.85 n.s.	-0.63	1.4 n.s.	11.72 ±1.0733	43.2 ±2.495	0.56366 ±0.02486

\*\*Significant @ 1 per cent.  
n.s. not significant.

Standard error of difference between seed fertility of 1 and 2 = 1.426.

Though the mean seed fertility in the controlled pollinated set appears to be somewhat higher than in the other sets, the differences are not statistically significant as shown by the homogeneity of the frequency distribution of all the individuals in seed fertility classes as shown in table 5.

TABLE 5

*The frequency distribution of plants in different seed fertility classes (number of seeds/siliqua)*

Material	Per cent frequency in seed fertility classes			Total number of plants studied
	0.1-10.0	10.1-20.0	20.1-30.0	
	seeds per siliqua			
1. Uncontrolled pollinated (diploid) .. ..	18.6	64.8	16.1	230
2. Polycross set .. ..	23.5	64.5	12.0	493
3. Restricted pollinated set .. ..	35.4	59.7	5.0	263
4. Controlled pollinated set .. ..	13.7	73.6	13.0	177

$$\chi^2_6 = 11.52 \quad P = 0.10 - 0.05.$$

The solitary instance of the female XI which did not show any correlation between seed number and siliqua size, needs to be considered. This absence of correlation would imply seed number to vary independently of siliqua size. Two situations leading to this result can be visualised. Either more seeds of smaller size could be packed into a siliqua of given length, or fewer seeds are farther spaced in the siliqua, than in the normal cases. The former would result in a lesser seed weight and the latter in lesser fertility. The fact that both in the restricted pollinated set and the controlled pollinated set the correlation coefficient was of the same order as in other sets indicated that the general trend of results in the females under open pollination was not different from that in the controlled crosses. Since in the former case all the females were considered together in estimating the correlation, it is likely that individual differences might have been obliterated. Therefore, a separate analysis of the females of the type XI only from the restricted pollinated set was made and the 'r' value was found to be 0.04 (not significant). Thus female XI behaves under open pollination in the same way as under assortative matings of the controlled pollinated set. We may now examine the female XI *vis a vis* the possible situations visualised earlier. The last column in table 1 is relevant here. It gives the unit siliqua length per seed, a datum obtained by dividing the mean siliqua length by the mean seed number. A comparison of this ratio in the different sets on the one hand and female XI on the other, would show whether the absence of correlation is due to spacing differences inside the siliqua. It is seen that female XI has a unit siliqua length of 3.543 mm. as against an overall mean of 3.285 mm. The difference is less than twice the standard error of the mean and hence not significant. On the other hand, female XI has a 100 seed weight of  $0.5149 \pm 0.251$  gms., significantly lesser than,  $0.5758 \pm 0.0249$  gms. of the rest of the females (standard error of difference = 0.29; difference between the means = 0.609). It appears, therefore, that the absence of correlation between seed number and fruit size in this female is a genetic characteristic (presumably smaller seed size) and not due to the male parents involved in the cross.

#### DISCUSSION

The primary object of this study is to find out whether there is any 'xenia' (metaxenia *sensu strictu*) in *Brassica* as reported by Singh (1957). Such an effect has not been reported before and the only published account of a similar study is that by Olsson (1960) who found no effect of the male parent on the oil content of the seeds in *Brassica* crosses. If the presumption that a metaxenia effect prevails is correct, it should be manifest as increased fruit size or seed size. Such an increase would depend on the male parent used; and in an experiment of the type under study, varying the degree of assortativeness of the matings should give rise to different relationships between fruit size, seed number and seed weight. The fact that such differences were not observed and that a uniform relationship between seed number and fruit size was noticed under all kinds of pollination indicates no metaxenia effects to be present. The high positive correlation between seed number and ovule number indicates that the former is determined by the genotype of the mother parent. This seed fertility in its turn determines the size of the fruit and both the characteristics are thus independent of the pollen. It is known that *Brassica* seeds, at the mature stage, are made up of about 98 per cent. hybrid tissue viz., cotyledons, radicle and plumule (Ahuja, 1958). There is practically no endosperm and the seed coat is probably the only maternal tissue involved. Consequently any increase in seed size must be due to cotyledons or other embryonal tissue and must be attributed to hybridity and cannot be termed as metaxenia or xenia. Increased rate of growth or total growth of the embryo should fall in the category of heterosis. In the present material, however, no indications of heterosis in seed weight was noticed in the restricted pollinated set.



Among the factors that affect embryo development the important role of maternal factors has been recognised. In the interspecific crosses in *Melilotus* (with non-endospermous seeds at the mature stage) the size of the hybrid embryo was found to be significantly correlated positively with the seed weight of the maternal parent (Long and Gory, 1960). Here probably a more efficient endosperm with its extra genome from the mother results in a larger embryo. An interesting observation in the present work is the positive correlation between seed weight and seed number in the controlled pollinated set. This is against general expectations. Olsson (1960) found that out of 15 correlations worked out between seed weight and number, in *Brassica* crosses, 14 were negative. A possible explanation of the different results reported here may be as follows. In the case of the autotetraploid material used in this work, the genes controlling seed size might not have reached their 'maximum efficiency' and consequently further enhancement of seed size independent of seed number should be possible. On the other hand, in the case of the diploids, the genes for seed size having reached their maximum efficiency, the seed size can be enhanced only at the expense of seed number.

From the foregoing it is evident that metaxenia (or 'xenia' of Singh, 1957) is probably not present in intra-specific *Brassica* crosses. This author does not specify whether the fruit size measured by him refers to the seed bearing portion only as in the present case, or includes the beak and pedicel. Even if metaxenia is present and results in an increase in the growth of the beak and pedicel, it can be of no consequence to seed yield. It has been suggested that the noticed effect was brought about by the diffusion of "hormonal substances or substances analogous to them in the tissue of the mother plant that constitute the seed and the fruit" (Singh, 1957). In as much as only the seed coat is maternal in origin, such an effect, even if present, would not make much difference in seed yield. It is well recognised that in the *Brassica* group of crops yield is influenced more by the number of seeds per silique than by seed weight (Schrimpf, 1954; Stolle, 1950; Olsson, 1960). Since the number of seed is a function of ovule number, which itself is determined by the genotype of the mother, the male parent is not likely to have any effect on seed yield. It, therefore, appears that there is little scope for the utilization of the phenomenon of metaxenia in the improvement of yield in the oleiferous *Brassicas*.

#### SUMMARY

This paper records the results of an attempt to find out whether any metaxenia effect is observed on the fruits and seeds in *Brassica* crosses as has been reported by Singh (1957).

Data on fruit size, seed number, and seed weight were collected on females of autotetraploid *toria* under pollination conditions varying from complete assortative to complete random matings. It was expected that metaxenia, if present, should be manifest as varying relationship between fruit size and seed number measured in terms of correlation coefficients between the two characters.

Fruit size was found to be correlated with seed number with same magnitude and sign over all the different types of pollinations, the 'r' value being 0.4. This relationship was not disturbed by varying the male parent. No metaxenia effect was observed.

Seed number per fruit at maturity is highly correlated with ovule number counted on the day of flower opening. This leads to the conclusion that seed number and fruit size are both dependent on ovule number which is determined ontogenically the earliest and by the genotype of the mother. In individual cases genetically determined small-seededness might disturb the correlation between seed number and fruit size.

It is concluded that there is little scope for exploiting metaxenia phenomenon in increasing the seed yield in oil *Brassicas*.

#### ACKNOWLEDGEMENTS

The authors are deeply indebted to Dr. A. B. Joshi, Dean of the Post Graduate School, I.A.R.I., formerly Head of the Division of Botany, I.A.R.I., New Delhi, for his keen interest in this study and for his constant encouragement. Thanks are due to the Indian Central Oilseeds Committee for sponsoring a Scheme at the Division of Botany, I.A.R.I., under which the observations reported herein were recorded. One of us (S.B.P.R.) is grateful to the Government of Mysore for deputation to the I.A.R.I., for post-graduate training. To Shri S. Ramanujam, Geneticist, I.A.R.I., thanks are due for a critical reading of the manuscript.

#### REFERENCES

- Ahuja, Y. R. (1958). Development and growth of embryo in *Brassica campestris* var. *toria*. *Curr. Sci.*, **24**: 205-06.
- Lang, R. C. and Gory, H. J. (1960). Factors affecting embryo development in crosses of *Melilotus officinalis* × *M. alba*. *Agron. J.*, **52**: 71-74.
- Olsson, G. (1960). Some relations between number of seeds per pod, seed size and oil content and the effects of selection for these characters in *Brassica* and *Sinapis*. *Hereditas, Lund*, **46**: 29-68.
- Schrimpf, D. (1954). Untersuchungen über den Blüten- und Schotenansatz bei Raps, Ruben und Senf. *Z. Acker- u. PflBau*, **97**: 305-36.
- Singh, D. (1957). Xenia and possibilities of its utilization in oleiferous *Brassicæ* for increasing yield. *Indian Oilseed J.*, **1**: 152-54.
- Stolle, G. (1954). Ein Beitrag zur Ertragszüchtung beim Winterraps. *Züchter*, **24**: 202-15.

# MEIOTIC ABNORMALITIES INDUCED BY X-RAYS IN *ARACHIS HYPOGOEA*

S. H. PATIL and K. C. BORA

*Biology Division, Atomic Energy Establishment, Trombay, Bombay*

THE groundnut (*Arachis hypogaea*) with a somatic chromosome complement of 40 (Husted, 1931; Patel and Narayana, 1937) is considered to be a polyploid (Darlington, 1948), for, there are species in this group with a somatic chromosome number of 20 (Mendes, 1947). Stebbins (1957) classifies it as a segmental allopolyploid.

During the course of studies on the cytogenetic effects of X-rays on groundnut, some interesting cytological abnormalities, especially those relating to the development of spindles and their activity, were observed. Besides describing various types of meiotic aberrations and discussing their significance in microsporogenesis, a special reference has been made in this communication to the mechanism of formation of multispindles.

It would seem from the meagre cytological data available on groundnut that sufficient investigations have not been carried out on the cytological aspects of the crop, probably because of the inherent difficulties encountered in handling such a material.

## MATERIALS AND METHODS

Dry seeds of *A. hypogaea* var. Spanish Improved, obtained from Agricultural College, Dharwar were irradiated with a series of X-ray doses ranging from 25,000 r to 75,000 r from a therapy type X-ray machine operating at 250 kVp, 30 mA with an inherent filter of 4 mm. aluminium. The seeds, arranged in a single layer, were placed at a distance of 18 cm. from the target and the dosage rate at that distance, as determined by a 100 r Victoreen chamber, was estimated to be about 2,500 r per minute.

X<sub>1</sub> plants were raised in pots. The dose 75,000 r was almost lethal with only about 10 per cent. survival. Two plants (nos. 304 and 534) from seeds receiving this dose showed about 45 and 85 per cent. pollen abortion respectively. Meiosis in these plants was studied after fixing the flower buds in acetic alcohol (1 : 3) and squashing the anthers in aceto-carmin.

## RESULTS

*Control.*—Observations showed chromosomal associations ranging from uni- to quadrivalents though associations other than bivalents were infrequent (about 0.15 per cell). A loose bivalent was invariably observed at late diakinesis in all the PMCs (Fig. 1).

The spindle at metaphase I was straight and narrow, as a result of which the chromosomes lying on the spindle appeared clumped. One of the bivalents at this stage was seen outside the normal group in about 15 per cent of the PMCs and it separated precociously at late MI. AI separation of the homologues was 'clean' except for a lagging bivalent (Fig. 2) in about 25 per cent. of the cells which, however, separated normally later. An interesting instance was observed in at least two PMCs where the homologues of laggards separated along different spindle fibres. It is believed that this can possibly happen when there is a segmental pairing with one of the distal segments of a homologue inverted in respect of spindle attachment. Chromosomal behaviour appeared to be normal in the subsequent divisional stages.



*Irradiated material : Plant no. 534.*—The main stem of this plant was fasciated and trifurcated in the later stages of development. Variation in the development of leaves with number of leaflets varying from 3-7 on each leaf was noted on this stem. The average rate of pollen abortion in the plant was as high as 75 per cent, the range of variation between the normal-looking branches arising from the unfasciated part of the stem and the fasciated stem being 66-85 per cent.

Diakinesis appeared to be an unfavourable stage for study because of the large number of chromosomes and their complex associations. Fragments and unoriented bivalents (Table 1), were present at MI (Fig. 3), the frequency of fragments varying from 1-2 and of bivalents from 1-3 per PMC. At least in two PMCs an unoriented multivalent of complicated nature was also noted.

TABLE 1

*Metaphase I abnormalities*

Dose—75,000 r Plant No. 534.

	PMCs with fragments only	PMCs with fragments and unorien- ted IIs	PMCs with unoriented IIs only	Normal PMCs	Total
No. of cells ..	5	16	5	26	52
Per cent. ..	9.6	30.8	9.6	50.0	100

Homologous separation at AI was abnormal with frequent occurrence of bridges, fragments and laggards, and the occurrence of bridge(s) with fragment(s) at anaphase has been considered to be the result of some types of crossover within the inverted segment of paracentric inversions. Bridges and fragments were observed in as many as 54.5 per cent. (Table 2) of the PMCs, four having two bridges and two fragments

TABLE 2

*Anaphase I abnormalities*

Dose—75,000 r Plant no. 534.

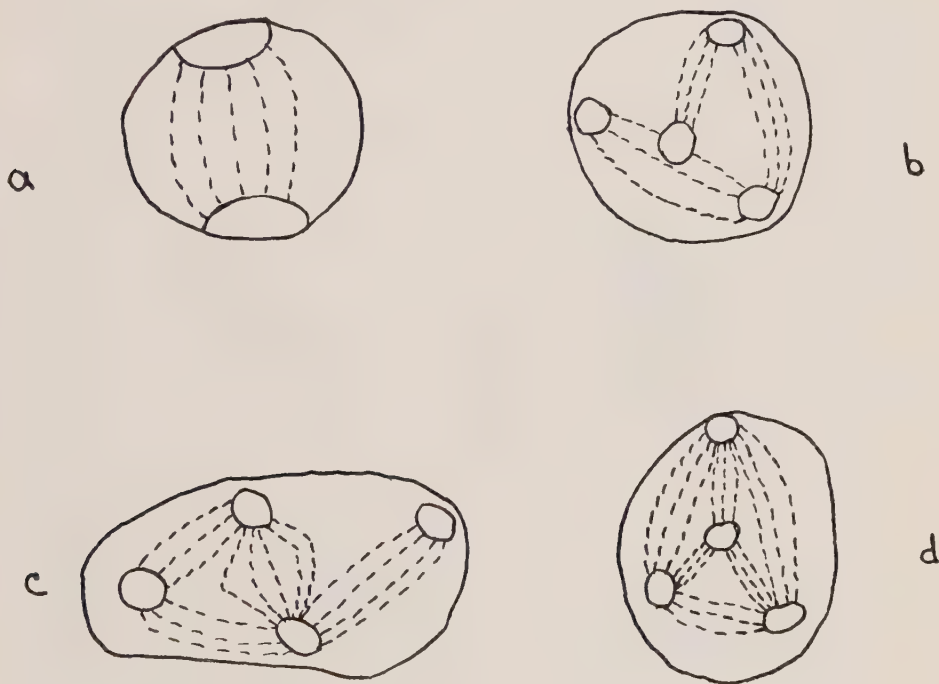
	PMCs with bridges, fragments and laggards	PMCs with bridges and fragments	PMCs with bridges and laggards	PMCs with bridges	PMCs with fragments	PMCs with laggards	Total
No. of cells	7	5	2	4	1	3	22
Per cent.	31.8	22.7	9.1	18.2	4.5	13.7	100

(Fig. 4) each. Each of the remaining PMCs, except two with bridges only, had a single bridge and a fragment (Fig. 5) presumably arising as a result of crossovers in an inversion loop. In cases where the bridges were without fragments it is probable

that the accompanying fragments were included in one or the other of the AI groups due to entanglement or attachment with the normal chromatids of the homologous chromosomes. The fragments may also be not visible if they are overlapped by the lagging chromosomes. One cell was observed with a fragment but without a bridge. This may be due to three strand double crossing over, one in the loop and the other between the loop and the centromere.

Lagging bivalents with frequencies varying from 1-3 per PMC were observed in about 54.6 per cent. of the cells. The occurrence of more than three lagging bivalents was rare.

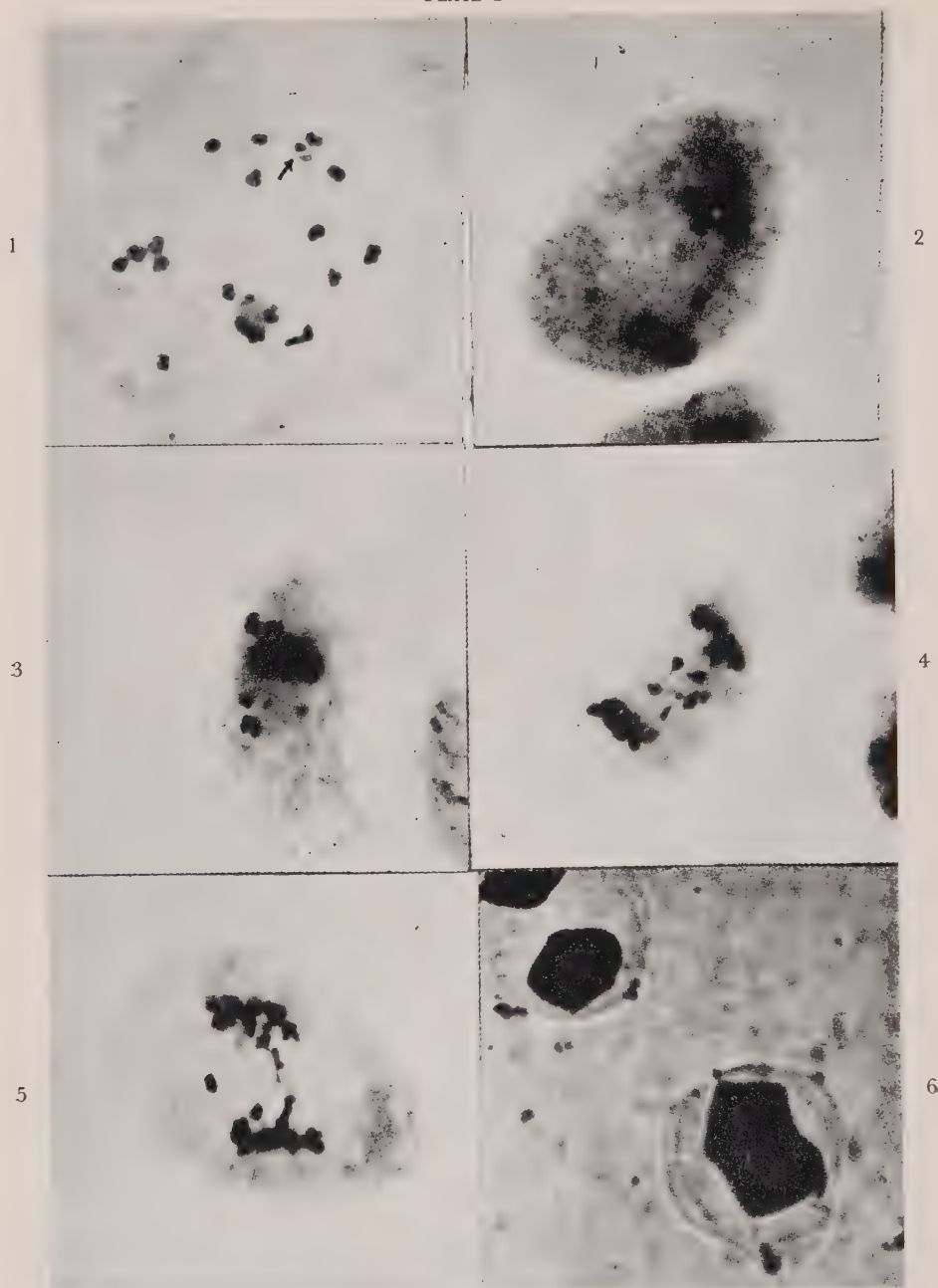
In addition to normal PMCs with four groups of chromosomes there were PMCs with only two (Text Figure 1a) groups of chromosomes. Even in PMCs with four groups of chromosomes, three or more spindles (Text Fig. 1, b-d) instead of two at the normal tetrad stage, developed around the four poles.



TEXT FIG. 1. a to d. PMCs from  $X_1$  plant no. 534. (Camera lucida diagrams). a. PMC at TII with only two groups of chromosomes and a large single spindle. b. PMC at TII with three spindles. c. PMC at TII with four spindles. d. PMC at TII with 6 spindles.

Besides chromosomal aberrations abnormal cytokinesis was fairly frequent (Table III). In normal plants cytokinesis takes place only after the completion of the second division as in *Paeonia*. Partial or complete failure of cytokinesis results in tetrad abnormalities (Figs. 6, 7 and 8) such as monads, diads, and triads. In the present case, the failure of cytokinesis was not only accompanied by the usual tetrad abnormalities but by additional micronuclei at a frequency of 1-2 per cell.

## PLATE I



FIGS. 1 and 2. From control plant. Fig. 1. PMC at diakinesis with a loose bivalent. Fig. 2. PMC at AI with a lagging bivalent.  
FIGS. 3 to 6. PMCs from  $X_1$  plant no. 534. Fig. 3. PMC at MI with unoriented bivalent and fragments. Fig. 4. PMC at AI with two inversion bridges and fragments. Fig. 5. PMC at AI with one inversion bridge and attached fragment. Fig. 6. A monad and a diad.



TABLE 3

*Tetrad abnormalities*

Dose—75,000 r      Plant no. 534.

	Monads		Diads		Triads		Tetrads		Total
	with micro- nuclei	without micro- nuclei	with micro- nuclei	without micro- nuclei	with micro- nuclei	without micro- nuclei	with micro- nuclei	without micro- nuclei	
No. of cells	2	27	27	38	3	15	16	114	242
Per cent.	0.9	11.1	11.1	15.7	1.2	6.3	6.6	47.1	100

Furthermore, there was an increase in the size of the pollen grains, the ratio between the irradiated and control varying from 1.0-1.5. Fused pollen grains were also observed (Fig. 9)

*Plant no. 304.*—This plant had abnormal leaf development during the early stages of growth but afterwards appeared normal. The abnormal leaves had 5 imparipinnate leaflets unlike the paripinnate arrangement met with in the control

Cytological abnormalities in this plant could be studied only in the second meiotic division. At interphase and MII there were frequently (Table 4) three groups of chromosomes in the PMCs (Fig. 10) instead of two as in controls and one group was always distinctly smaller than the others. The number of chromosomes in the smallest group varied between 3-8, cells with groups of 8 chromosomes being more frequent. At least one of the large groups had about 20 chromosomes at MII. Development of multispindles (Fig. 11) was also noticed in this plant. One or two unoriented chromosomes (Fig. 12) were seen at late MII in some PMCs.

TABLE 4

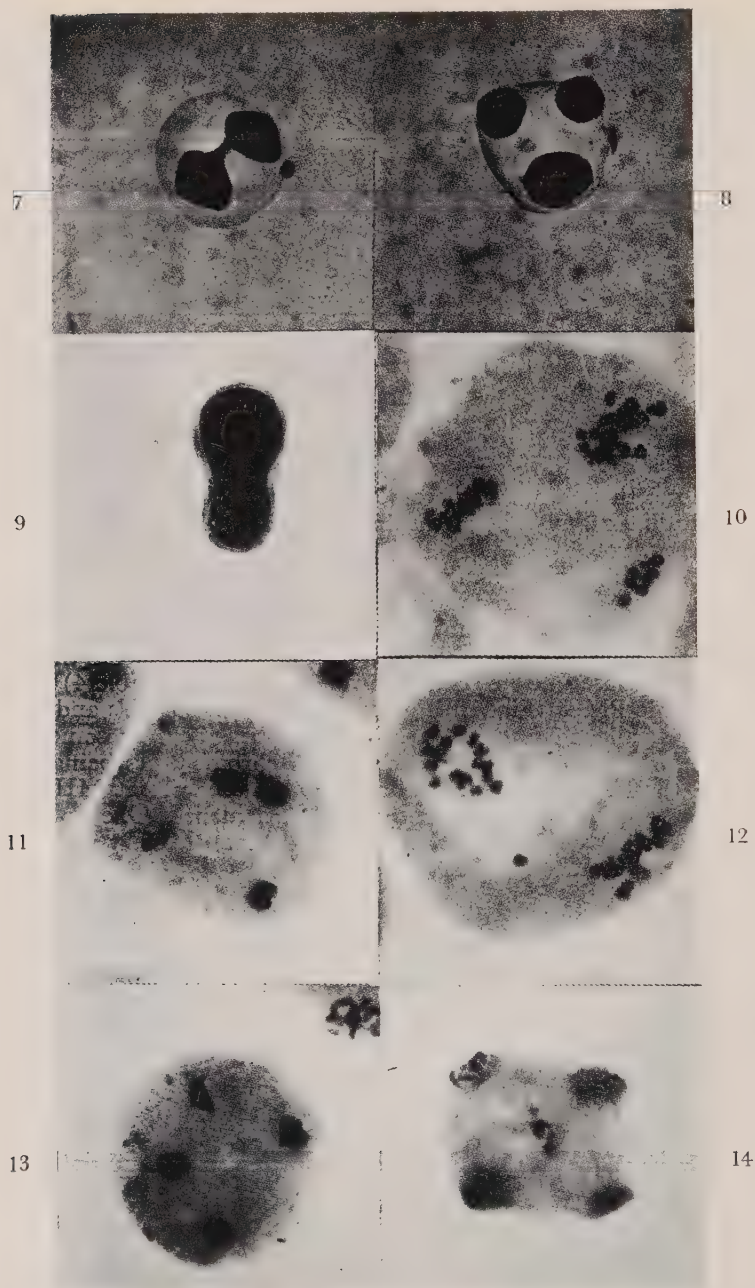
*Metaphase II abnormalities*

Dose—75,000 r      Plant no. 304.

		PMCs with 3 chromosomal groups	PMCs with unoriented chromosomes	Normal PMCs	Total
No. of cells	..	10	7	20	37
Per cent.	..	27.1	18.9	54.0	100

Persistent AI bridges have been observed in about 2.8 per cent of PMCs at AII. Bridges, presumably arising due to paracentric inversions, were observed at AII in about 8.6 per cent of PMCs (Table 5).

## PLATE II



FIGS. 7-9 From plant no. 534. Fig. 7. A diad with incomplete wall development. Fig. 8. A triad. Fig. 9. A fused or twin pollen grain.

FIGS. 10-14 From plant no. 304. Fig. 10. PMC at MII with three groups of chromosomes. Fig. 11. PMC at TII with three spindles one of which is smallest having only a chromosome at each pole. Fig. 12. PMC at MII with unoriented chromosome. Fig. 13. PMC at TII with four spindles around four poles. Fig. 14. PMC at TII with complicated spindle development.

TABLE 5

*Anaphase II abnormalities*

Dose—75,000 r

Plant no. 304.

		PMCs with bridges	PMCs with laggards	PMCs with persistent bridge	Normal PMCs	Total
No. of cells	..	3	1	1	30	35
Per cent.	..	8.6	2.8	2.8	85.8	100

In addition to the irregularities in chromosomal orientations and bridge formation, abnormal development of spindle was also observed in some PMCs. Unlike two in the control, in one cell there were three independent spindles; one of them was small with only a single chromosome at each pole. It seems possible that this additional spindle might have developed from an unoriented chromosome associated with supernumerary poles or spindle organisers at MII. An interesting instance of development of multispindles was noted in another cell where there were four spindles with only four poles (Fig. 13), the spindles developing around the poles and connecting all of them. Among others there was one PMC with a very complicated spindle development (Fig. 14). It had an abnormal separation of chromosomes with 3-4 chromosomes in the middle of the tetrad structure resembling a pentad formation.

Pollen abortion in this plant was about 45.6 per cent. and the range of pollen size variation was the same as in the control, but the pod setting was only partial.

## DISCUSSION

The cytological irregularities observed in the control fully substantiate the previous views regarding the genetic make up of groundnut. It is certain that groundnut is not a normal diploid but a tetraploid, perhaps with segmental interchanges.

It is noteworthy that meiotic abnormalities such as increasing frequency of lagging chromosomes, failure of cytokinesis, increase in the size of pollen grains, irregular chromosome separation, pollen sterility, spindle abnormalities etc., commonly observed in interspecific hybrids can be induced by X-rays.

It has been suggested (Janick and Stevenson, 1955) that abnormal cytokinesis is due to laggards at AI, but Darlington (1937) is of the view that the formation of cell-wall depends on spindle activity. Khoshoo (1957) is also of the opinion that the failure of spindle may lead to failure of cytokinesis. In groundnut, however, such a clear correlation cannot be established. The frequency of PMCs with abnormal cytokinesis was about 52.9 per cent. which, incidentally, agrees with the observations of Khoshoo (1957) in conifers (spontaneous aberration). The consequent effect observed in conifers was about 90 per cent. pollen abortion as compared to 85 per cent. in groundnut. It should be pointed out that the same degree of pollen abortion in groundnut and conifer may be, perhaps, a mere coincidence and the cause may be different. While the failure of cytokinesis in conifers was due to the failure of spindle formation, in groundnut it may be due to some action of radiation; for, clear spindle structure was seen at MI, AI and AII,



The increase in the size of pollen grains may be related to increased number of chromosomes in them (Darlington, 1937; Janick and Stevenson, 1955), resulting, possibly from the radiation induced failure of cytokinesis. A few fused or twin pollen grains, most of which aborted, were also observed. Bhaduri and Natarajan (1956) have also observed such pollen grains in wheat after treating with nitrogen mustard. They concluded that such grains developed due to sticky bridges connecting the two nuclei. The present observations, however, do not substantiate this.

The occurrence of persistent AI bridges can be taken as an evidence (Darlington and La Cour, 1941; Carson, 1946) of the presence of inversion bridges at AI. It may be of interest to point out that Rhoades and Dempsey (1953) also observed AII bridges in 8.6 per cent. of maize PMCs. But, whereas in maize the corresponding rate of pollen abortion was about 22 per cent., in groundnut it was as high as 45 per cent. However, the high rate of pollen abortion in groundnut may not be due to bridge formation alone. Other abnormalities such as unoriented chromosomes at MII and laggards at AII may also give rise to aneuploid spores of uncertain viability. Moreover, since it is a plant raised from an irradiated seed, radiation may also act through processes other than those mentioned above (Sparrow, 1951).

Tripolar separation of chromosomes at AI as found in groundnut has been observed in interspecific hybrids (Smith, 1936; Walters, 1958) and attributed to the development of tripolar spindle at AI. It has also been suggested (Darlington and Thomas, 1937) that incompact spindle results in the divergence of groups of chromosomes to form 3-4 TI nuclei. The occurrence of abnormal spindles of a wide range observed at TII in groundnut would perhaps indicate that there was an abnormal development of spindle at AI also. That this might be so was shown by the development of 6 poles at AII. The expected tetrad abnormalities, such as the formation of polyads after separation of daughter chromosomes at AII were not observed, indicating the possibility that this type of separation of chromosomes was lethal.

One of the interesting findings is the occurrence of multispindles and their mode of orientation. It has been assumed that spindle organizers or polar bodies function in association with centromeres in organising the spindle structure (Darlington 1937; Hughes, 1951; Walters, 1958) and that the spindle is organised through the action of centromeres and pole determinants (Swanson and Nelson, 1942 and Mazia, 1956). Fankhauser (1934a) observed that in the absence of centromeres, the spindles formed were narrower than normal but Walters (1958) suggested that the presence of one centromere at least was necessary for the organization of the spindle.

It has been considered by Schrader (1953) that the multipolar origin of spindle, not directly associated with chromosomes, was difficult to interpret on almost any basis. In the light of the above statement a classical interpretation of spindle anomalies in groundnut might appear to be extraordinarily difficult. But the mere assumption that the spindle organization necessarily required not only the polar bodies but centromeres also cannot fully explain the occurrence of PMCs with three or four spindles around common poles. The absence of abnormal groupings of chromosomes at TII would obviously rule out the hypothesis of incompact spindle.

The presence of three or four spindles in a PMC having only four chromosomal groups at TII would apparently imply that two of them had developed in relation to two MII plates and daughter poles and the rest between sister poles. The occurrence of PMCs with only one large spindle at TII might possibly be due to failure of chromosomes to go through AII and TII and persistence of AI spindle.

It is known that the spindle consists of two types of fibres, one running between poles and the other between the pole and the centromere. It is also known that the spindle structure is mostly organized in the cytoplasmic substrate of a cell. It is, however, not certain how far the centromeric activity can influence the structural

organization of the spindle. Nor, is it known, whether this affects the organization of fibres running between centromeres and poles alone or those between poles as well.

### SUMMARY

Cytological investigations have been made on  $X_1$  groundnut plants raised from seeds exposed to 25,000 r and 75,000 r of 250 kVp X-rays. The observations revealed that there occurred:

- (i) a large number of reciprocal translocations leading to the formation of chain and ring multivalents,
- (ii) inversions leading to fragmentation and bridges at AI and AII and persistent AI bridges at TII,
- (iii) abnormal spindles, sometimes with irregular chromosomal separation,
- (iv) partial or complete failure of cytokinesis leading to the formation of bigger pollen grains and also fused or twin pollen grains.

### REFERENCES

- Bhaduri, P. N. and Natarajan, A. T. (1956). Studies on the effects of *Nitrogen mustard* on chromosomes in somatic and gametic plant tissues. *Indian J. Genet.*, **16**: 8.
- Carson, H. L. (1946). Selective elimination of inversion dicentric corticoids during meiosis in the eggs of *Sciara impatiens*. *Genetics*, **31**: 95.
- Darlington, C. D. (1937). "Recent advances in cytology". J. & A. Churchill Ltd., London.
- (1948). Groundnut breeding. *Nature* (London), **162**: 621.
- and LaCour, (1941). Genetics of embryosac development. *Ann. Bot., N. S.*, **5**: 547-56.
- and Thomas, P. T. (1937a). The breakdown of cell division in a *Festuca-Lolium* derivative. *Ann. Bot., N. S.*, **1**: 747-761.
- Fankhauser, G. (1934a). Cytological studies on egg fragmentation of the *Salamander triton*; the cleavage of egg fragments without the egg nucleus. *J. exper. Zool.*, **67**: 349.
- Hughes, A. F. (1951). "The Mitotic Cycle. The cytoplasm and nucleus during interphase and mitosis". Butterworths, London.
- Husted, L. (1931). Chromosome number in the species of peanuts. *Amer. Nat.*, **65**: 476.
- Janick, J. and Stevenson, C. (1955). The effects of polyploidy on sex expression in spinach. *J. Hered.*, **46**: 151.
- Khoshoo, T. N. (1957). Cytology of Conifers: III. Partial failure of meiotic spindle in *Cephalotaxus drugacea* var. *pedunculata*. *Cytologia*, **22**: 80.
- Mazia, D. (1956). The life history of the cell. *Amer. Scientist*, **44**: 1.
- Mendes, A. J. I. (1947). Estudios citologicos no genero *Arachis* (quoted from Darlington, *Nature*, (London), **162**: 621, 1948).
- Patel, J. S. and Narayana, G. V. (1937). Chromosome number in some economic plants. *Curr. Sci.*, **5**: 470.
- Rhoades, M. M. and Dempsey, E. (1953). Cytogenetic studies of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. *Amer. J. Bot.*, **40**: 405.
- Schrader, F. (1953). *Mitosis: The movement of chromosomes in cell division*. Columbia University Press, New York.
- Smith, L. (1936). Cytogenetic studies in *Triticum monococcum* L. and *T. aegilopoides*. *Bull. Res. Bull.*, **248**: 487.
- Sparrow, A. H. (1951). Some cytological and morphological changes induced by ionizing radiations in plants. *Science*, **114**: 487.
- Stebbins, G. L. (1957). Genetics, Evolution and Plant Breeding. *Indian J. Genet.*, **17**: 129.
- Swanson, C. P. and Nelson, R. 1942. Spindle abnormalities in *Mentha*. *Bot. Gaz.*, **104**: 273.
- Walters, M. S. (1958). Aberrant chromosome movement and spindle formation in meiosis of *Bromus* hybrids: An interpretation of spindle organization. *Amer. J. Bot.*, **45**: 271.

# MUTATION STUDIES IN ANNUAL CHRYSANTHEMUM—I. RADIATION-INDUCED VARIATION IN FLOWER FORM

H. K. JAIN, A. K. BOSE, D. SATHPATHY and S. C. SUR

*Division of Botany, Indian Agricultural Research Institute, New Delhi-12*

A large number of studies have been reported in recent years on the use of radiation-induced mutations in the improvement of crop plants. Similar investigations on other groups of plants have, however, been relatively few. The present experiments on *Chrysanthemum carinatum* were undertaken, keeping in view the consideration that while the possibilities and limitations of this approach remain to be clearly defined by further work, mutations affecting one or two characters rather than the overall agronomic potentiality of plants can, in general, be planned with greater chances of success. The seed propagated annual species of *Chrysanthemum*, unlike the vegetatively multiplied perennials, are not very popular mainly because of the less attractive form, size and colour of their flowers. The present species has been found to be self-incompatible and has 18 as its diploid chromosome number.

## MATERIALS AND METHODS

Because of the highly heterozygous condition of the plants—an outcome of their breeding system—*Chrysanthemum carinatum* presents obvious difficulties as a material for mutation studies. Keeping this fact in view, more than 600 control plants of the selected variety have been analysed for phenotypic variation, particularly in respect of flower form. The radiation treatment consisted of exposing the seeds to an X-ray dose of 15,000 r at an operating voltage of 50 kV. The 535  $X_1$  plants, obtained from a total of 1,000 treated seeds, were grown in the field under conditions comparable with those for the control material. The  $X_2$  and  $X_3$  progenies were raised from selected  $X_1$  and  $X_2$  plants respectively. It was found difficult to undertake control pollinations under field conditions and the  $X_1$  and  $X_2$  plants were therefore left to open-pollinate in isolation of the control material. The  $X_4$  progenies, on the other hand, were raised from a number of selected  $X_3$  plants which were control-pollinated.

The single (1), semi-double (3-5) and double (6-14) type of flower forms have been classified on the basis of the number of whorls of ray-florets indicated in parenthesis. Flowers having two distinct whorls of petals were not observed although it was not uncommon to find single type of flowers with extra number of petals, particularly in the treated material. In those cases where many petals were produced without being arranged in distinct whorls, their number was taken into consideration for the purpose of classification. It has been found convenient in the following account to use the words flower and ray-florets interchangeably with inflorescence and petals, respectively.

## RESULTS

### (i) Control and the $X_1$ plants:

The viability of seeds following the radiation treatment was not drastically affected; 53.5 per cent. of them, compared with 64.5 per cent. of the controls, showed germination. The  $X_1$  plants were as vigorous as the controls although their height was reduced, giving them a bushy appearance. A more characteristic radiation effect was observed in the lack of uniform chlorophyll distribution in the leaves of 5 per cent.



of the plants. As regards the more important character of flower form, nearly 4 per cent. of the  $X_1$  plants differed from the controls in having an increased number of ray-florets. In only two of these plants however, the number was adequate to give the inflorescence a double appearance. All the control plants have been found to produce single type of flowers having in most cases 21 petals (Fig. 1). The control plants grown over different years have shown no deviation from this pattern. The single nature of flower form in this variety was also recorded by Mr. H. B. Singh of the Botany Division, I.A.R.I., who kindly supplied seeds for this study from his multiplication plot.

(ii) *Flower form variation in  $X_2$  and  $X_3$  generations:*

**$X_2$ .**—The effect of radiation treatment on flower form, indicated to some extent by the above observations, was exhibited more fully in the  $X_2$  generation. A wide range of variation affecting this character was shown by a number of these plants. The double flowers produced by some of the  $X_2$  plants were far more striking than those on the two  $X_1$  plants, both in respect of the number and the arrangement of their ray-florets. As many as 14 whorls of petals were produced in some of them. In others, the flowers were characterised by tubular shape of their petals, a character generally associated with the vegetatively propagated perennial species.

The  $X_2$  population was obtained from 18  $X_1$  plants, which either showed semi-double or double type of flowers or other morphological abnormalities described above. It would have been, obviously, desirable to raise a larger number of  $X_2$  progenies but this was not found possible on account of limitations of space. The  $X_1$  plants, however, were left to open-pollinate and to some extent therefore, seeds obtained from the selected lot, with their differing genotypes, can be considered as representative of the population as a whole.

**Doubles.**—The double type of flowers produced on different  $X_2$  plants were not all similar. Two distinct types could be recognised. The first showed the ray-florets arranged in discrete whorls giving the inflorescence a regular appearance (Fig. 2). The second type of doubles had their petals arranged not in distinct whorls but rather closely crowded together resulting in a compact appearance of the inflorescence (Fig. 3). The increase in the number of ray-florets was found to be achieved at the expense of the inner disc-florets whose number was reduced. Apart from the plants showing double flowers, a number of  $X_2$  plants produced semi-double type of inflorescences.

**Tubulars.**—The  $X_2$  plants showing tubular petals were also of two types—those which had all their flowers uniformly and completely tubular (Fig. 4) and others in which this condition was partly manifested. In the latter type, with the exception of a few flowers which may be completely tubular, a varying number of tubular and non-tubular ray-florets are present in the inflorescence. The usual pattern was that all the petals of the first few flowers were uniformly tubular but this condition tended to break down to a greater or lesser extent in the later produced inflorescences, which consequently are of a mixed type.

**$X_3$ .**—The double and tubular type of flowers produced on the  $X_2$  plants were reproduced in the  $X_3$  progenies. The double condition in these  $X_3$  plants was very similar to that in the  $X_2$ . Both regular and compact type of double were present. The tubular form in the different  $X_3$  plants, on the other hand, showed considerable variation not observed in the  $X_2$  cultures. Some of the  $X_3$  plants showing this type of inflorescence had their petals turned tubular along their entire length. Open-tipped or half-formed tubes were present in the inflorescences of some of the others.

(iii) *Frequency of doubles and tubulars:*

As the  $X_1$  and  $X_2$  parental plants set seeds under condition of open pollination, observations on the frequency of plants showing different type of flower forms in the

$X_2$  and  $X_3$  progenies are only of limited interest from the genetic point of view and will not be considered here.

The  $X_4$  progenies, in contrast to the  $X_2$  and  $X_3$ , are of greater interest as these were raised from selected  $X_3$  plants whose pollinations were experimentally controlled, although the field conditions under which this was done were not very satisfactory. The segregation of plants showing different types of flower forms in these progenies is given in table 1.

TABLE 1

*Showing segregation of plants with different types of flower-forms in  $X_4$  progenies*

$X_4$ progeny No.	Flower form in the $X_3$ female and male parents	No. of $X_4$ plants showing different type of flower forms			
		Single (control type)	Double	Semi-double	Tubulars
1	Double $\times$ Double	6	5	4	..
2	Double $\times$ Double	2	3	11	..
3	Double $\times$ Semi-Double	6	23	5	..
4	Double $\times$ Semi-Double	7	22	4	..
5	Semi-double $\times$ Semi-double	16	60	111	..
6	Tubular $\times$ Tubular	2	..	3	56
7	Tubular $\times$ Tubular	8	..	9	49
		47	113	147	105

A number of  $X_3$  and  $X_4$  progenies from open pollinated plants are also of interest, though for a different reason. Some of the plants in these showed new types of flower forms which are obviously the result of hybridisation between double and tubular types. The inflorescence in these combine the double condition with tubular shape of the ray-florets (Fig. 5). These partly or completely tubular double flowers appear more attractive than either the non-tubular doubles or the tubular singles.

The pollen and seed fertility of  $X_2$ ,  $X_3$  and  $X_4$  plants was not found to be very much affected compared with that in the control material. Most of the  $X_4$  plants showing altered flower forms had over 80 per cent. pollen fertility compared with 95 to 100 per cent. in a corresponding group of controls. Interchange heterozygosity, indicated by the presence of multiple associations of chromosomes, was found to be present in a large number of plants in the treated cultures. Multiple associations, however, were also found to be present in some of the control plants when a large number of them were analysed, although these mostly showed a single configuration of 4 chromosomes in contrast to the multiples of six or two multiples of four commonly found in the treated group (Fig. 6).

#### DISCUSSION

Radiation-induced changes in flower parts have been described previously in a number of plants. In most cases, when the treatments were given to growing plants, these have been found to be due to physiological disturbances rather than to gene



PLATE I



FIG. 1. Single flower form (control type) with one whorl of ray-florets  $\times 1.5$ .  
FIG. 2. Mutant flower form (regular type double)  $\times 1.4$ .  
FIG. 3. Mutant flower form (compact type double)  $\times 1.8$ .  
FIG. 4. Mutant flower form (tubular type)  $\times 1.2$ .



## PLATE II

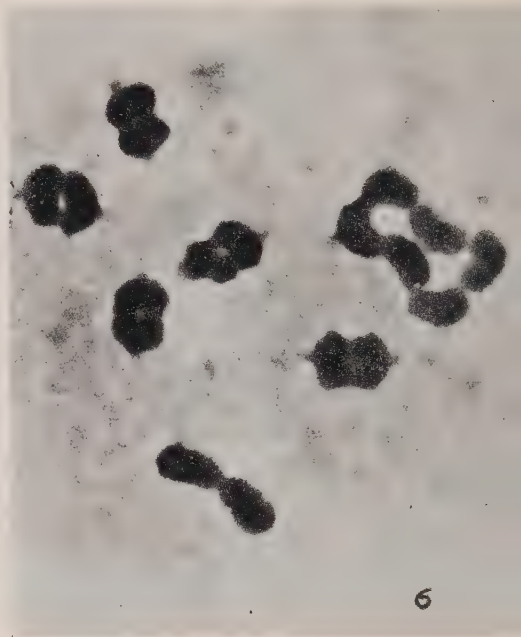


FIG. 5. Mixed tubular double (recombinant)  $\times 1.6$ .

FIG. 6. Pollen mother cell showing one multiple-association of 6 chromosomes and 6 bivalents  $\times 1530$ .

mutations (Gunckell and Sparrow, 1953; Gunckell, 1957; Johnson, 1931). Heritable changes affecting flower characters have been produced among other plants in tobacco (Goodspeed, 1929), *Antirrhinum* (Stubbe, 1960) and carnation (Sagawa and Mehlquist, 1959). The present observations on annual chrysanthemum show that the X-ray induced changes in flower form are genetically determined. It was possible to suggest this from observations on the  $X_3$  plants; the  $X_4$  progenies provide confirmatory evidence.

The more conspicuous type of doubles and the tubular flowers were first observed in a number of  $X_2$  plants. Both these flower forms were found to be reproduced in the  $X_3$  progenies with increased frequency. This increase can obviously be attributed to the fact that the  $X_3$  progenies were raised from selected  $X_2$  plants showing double or tubular type flowers. The  $X_2$  plants on the other hand, were raised from  $X_1$ , only a few of which had extra number of petals in their flowers. The  $X_4$  progenies, raised as these were from selected  $X_3$  plants whose pollinations were controlled, are of greater value, as already pointed out, in showing the nature of the induced changes in flower form. In these, plants having double or tubular type of flowers for which the  $X_3$  parents were selected predominate, thereby providing evidence that the changes in flower form are hereditary in nature. The occurrence of a few plants producing control type flowers in these progenies could be due to stray pollination. As has already been indicated, the field conditions under which controlled pollinations were done were not very satisfactory. Alternatively, their occurrence may be a function of the induced genetic changes, whose precise nature remains to be determined.

The induced variation in flower form may, next, be considered in relation to the naturally occurring variability for this character. While little is known about the course of evolution in the annual types, the more popular perennial or the garden varieties of *Chrysanthemum* have received considerable attention from this point of view. It is generally recognised that in the wild state all *Chrysanthemum* blooms were single flowers which subsequently gave rise to the double types (Wilson, 1951). It seems reasonable to suppose that floral variation along similar lines has occurred in annual varieties. Both single and double type varieties are common in *C. carinatum* and other annual species. Beyond this level, however, the perennial species appear to have advanced at a much faster rate. The tremendous variability in flower form (conditioned by the number, shape and arrangement of petals) and colour characteristic of the garden varieties is lacking in the annual types. Coats (1956) in his 'Histories of Flowers' refers only to double and single type of flowers in the annual species. The tubular-petalled flowers, which constitute such an important class in the perennial species, are not commonly known to occur in the annual group. The present observations on X-ray induced variation would suggest that partly at least this may be due to our failure to make suitable selections rather than to a complete lack of variation. In particular, the tubular character of the ray-florets in combination with the double condition, offers considerable scope for evolving attractive annual varieties. The single type of tubular flowers isolated in the  $X_2$  population are not very attractive. However, the double tubulars, which occur in  $X_3$  and  $X_4$  generations as recombinants, are of considerable interest.

In emphasising the range of variation in annual chrysanthemum, it is not the intention to suggest that this variability is in any way comparable to that in the perennial species. The two groups of varieties, although belonging to the same genus, seem to have acquired their variability through different mechanisms. All the garden chrysanthemums appear to have been derived from hybrids within a hexaploid complex of Chinese species, the most important of which is *C. indicum* (Darlington, 1956). Dowrick (1953) from observation on several related clones, has concluded that variation in chromosome number in somatic tissue, arising from irregularities of mitotic division, has played an important part in the evolution of bud sports, particularly those showing new colours. The role of numerical and structural changes of chromosomes in giving new types in this group has also been indicated by the studies of Sampson *et al.* (1958). Furthermore, increase in chromosome number by polyploidy has been found to be associated with increase in bloom size. Both *C. carinatum* and *C. coronarium*, the two important annual species, are diploid and sexually reproduced and have not had the same opportunities for the origin and preservation of variation.

#### SUMMARY

1. Radiation induced phenotypic variation including several interesting changes in flower form, has been described in annual chrysanthemum.
2. Evidence based on observations on  $X_4$  cultures has been presented which shows that the induced changes in flower shape are genetically determined.
3. A recombinant form combining the tubular shape of the petals with the double condition has been obtained which appears more attractive than either the control or the induced mutant types.
4. The results have suggested that variation in annual chrysanthemum offers considerable scope for selecting and synthesising new varieties.
5. The evolutionary processes responsible for the occurrence of variation in annual and perennial species of *Chrysanthemum* have been discussed and the mechanism responsible for the greater flexibility characterising the latter group indicated.

## ACKNOWLEDGEMENTS

We are thankful to Dr. B. P. Pal and Dr. A. B. Joshi for providing facilities and for continued interest and encouragement during the progress of this work. Our thanks are also due to Dr. M. S. Swaminathan for a discussion of the results with us.

## REFERENCES

- Coats, A. M. (1956). *Flowers and their Histories*. Hulton Press, London.
- Darlington, C. D. (1956). *Chromosome Botany*. Allen & Unwin Ltd., London.
- Dowrick, G. J. (1953). Chromosomes of *Chrysanthemum*. II. Garden varieties. *Heredity*, **7**: 59-72.
- Goodspeed, T. H. (1929). Cytological and other features of variant plants produced from X-rayed sex cells of *Nicotiana tabaccum*. *Bot. Gaz.*, **87**: 563-82.
- Gunckel, J. E. (1957). The effects of ionising radiations on plants. Morphological effects. *Quart. Rev. Biol.*, **32**: 46-56.
- , Morrow, I. B., Sparrow, A. H. and Cristensen, E. (1953). Variation in the floral morphology of normal and irradiated plants of *Tradescantia paludosa*. *Bull. Torrey. bot. Cl.*, **80**: 445-56.
- Johnson, E. L. (1931). Effect of X-irradiation upon growth and reproduction of tomato. *Plant Physiol.*, **6**: 685-94.
- Sagawa, Y. and Mehlquist, G. A. L. (1959). Some X-ray induced mutants in the Carnation (*Dianthus caryophyllus*). *J. Hered.*, **50**: 78-80.
- Sampson, D. R., Walker, G. W. R., Hunter, A. W. S. and Bragdo, M. (1958). Investigations on the sporting process in greenhouse chrysanthemums. *Canad. J. Pl. Sci.*, **38**: 346-56.
- Stubbe, H. (1959). Some results and problems of theoretical and applied mutation research. *Indian J. Genet.*, **19**: 13-29.
- Wilson, G. F. (1951). *R.H.S. Dictionary of Gardening*, Clarendon Press, Oxford, **I**: 472-73.



STUDIES IN INTERSPECIFIC AND INTERGENERIC HYBRIDS OF *SACCHARUM*—II. STAMINAL STERILITY IN CERTAIN F<sub>1</sub> HYBRIDS WITH *S. SPONTANEUM* AS THE PISTIL PARENT\*

P. A. KANDASAMI

*Sugarcane Breeding Institute, Coimbatore*

INSTANCES of male sterility resulting from the interaction between the cytoplasm of one species and the nuclear contents of others have been reported in the genus *Begonia* by Villerts (1942, quoted by Edwardson, 1956), in *Nicotiana* by Clayton (1950) and also by Koopmans (1955) in interspecific crosses between *Solanum chacoense* and *S. rybinii*. In the interspecific and intergeneric crosses studied by the author, staminal sterility appeared characteristically in certain combinations when *S. spontaneum* was the pistillate parent, confirming the findings of Raghavan (1951). In all cases, reciprocal crosses gave fertile plants only.

In the present study, varieties belonging to three species of *Saccharum*, namely, *S. officinarum*, *S. barberi* and *S. robustum* as well as some sugarcane varieties of hybrid origin (Co. 205, Co. 285, Co. 421, Co. 467, CAC 87 and POJ. 2725) were used. Also, a few related genera, viz., *Sclerostachya*, *Narenga*, *Erianthus* and *Sorghum* were crossed with *S. spontaneum*.

As many as 484 seedlings raised from 40 combinations, comprising of intraspecific, interspecific and intergeneric crosses with *S. spontaneum* as one of the parents, were studied. The degree of staminal sterility exhibited in different combinations of parents was not uniform. The tendency was pronounced when *S. officinarum* as well as the related genera were used as pollen parents and absent when *S. robustum* was so used, while in the crosses, *S. spontaneum* × *S. barberi* and *S. spontaneum* × sugarcane varieties of hybrid origin, there was little or no tendency towards such staminal sterility. In intraspecific crosses of *S. spontaneum*, the progeny were found to be fertile.

The staminal sterility appeared in varying degrees, one, two or all the three anthers being transformed into pistil-like structures. At times, there were apical, stigma-like papillae on the anthers.

With greater and greater modification of the stamens, there was a corresponding reduction in the quantity of pollen produced. In spite of this, fairly regular meiotic divisions of the pollen mother cells and production of fertile pollen were observed in the unaffected portions of the anthers. In some plants, even though the anthers were normal, one, two or all the three anthers possessed apical stigma-like papillae. They were scored as plants with normal anthers. In certain crosses involving related genera, viz., *S. spontaneum* SES 184A × *Sclerostachya*, *S. spontaneum* SES 184A × *Narenga*, *S. spontaneum* SES 248 × *Sclerostachya* and *S. spontaneum* SES 248 × *Narenga*, the anthers, though normally developed, failed to dehisce and the pollen grains were found to be agglutinated. As stated above, staminal sterility was altogether absent in reciprocal crosses i.e., where *spontaneum* was the staminate parent.

The expression of staminal sterility observed in these crosses was found to vary with the male parent. The tendency was very pronounced when either *S. officinarum* or the related genera were used as pollen parents, though there were varietal differences with regard to the extent of modification. It was notably absent when various geographical races of *S. spontaneum* were used as pistil parents and *S. robustum* as the pollen source. This may, perhaps, be construed as indicating a qualitative similarity

\* Part of a thesis submitted for the M. Sc. degree of the Madras University.

of the *S. robustum* nuclei with those of *S. spontaneum*, at least in respect of the fertility loci. This is in agreement with the suggestion made by Parthasarathy (1951) that *S. robustum* is derived from a natural cross between *S. officinarum* and *S. spontaneum*. The appreciable amount of compatibility of the *S. barberi* genome with the *spontaneum* cytoplasm is probably to be attributed to the presence of *S. spontaneum* chromosomes in the nuclei of the former, as suggested by Parthasarathy (1946). The very similar behaviour of a number of Coimbatore canes of hybrid origin is according to expectation as they contain *spontaneum* chromosomes in varying numbers.

#### ACKNOWLEDGEMENTS

I am indebted to Dr. T. S. Raghavan, Retired Second Cané Breeding Officer, Sugarcane Breeding Institute, Coimbatore and the late Shri N. L. Dutt, ex-Director, Sugarcane Breeding Institute, Coimbatore for their guidance in conducting this study. I am grateful to Dr. N. R. Bhat, Director, Sugarcane Breeding Institute, Coimbatore for making valuable suggestions in writing up the article.

#### REFERENCES

- Clayton, E. C. (1950). Male sterile tobacco. *J. Hered.*, **41**: 171-75.  
Edwardson, J. R. (1956). Cytoplasmic male-sterility. *Bot. Rev.*, **22**: 696-738.  
Koopmans, A. (1955). Changes in sex in the flowers of the hybrid *Solanum rybinii* × *S. chacoense*. III. Data about the reciprocal cross *Solanum chacoense* × *S. rybinii*. *Genetica*, **27**: 465-71.  
Parthasarathy, N. (1946). Origin of North Indian sugarcanes. *J. Indian bot. Soc.*, M.O.P. Iyengar Comm. Vol., 133-50.  
——— (1951). Some cytogenetical aspects of the origin of sugarcane. *Indian J. Genet.*, **11**: 63-66.  
Raghavan, T. S. (1951). Cytoplasmic inheritance in *Saccharum*. *Curr. Sci.*, **20**: 138-40.

## GENETICA AGRARIA

A Journal of Genetics applied to the Agriculture edited by "Centro di Genetica del Consiglio Nazionale delle Ricerche" and "Società Italiana di Genetica Agraria", Pavia, Italy.

The Journal is issued four times a year. Each volume about 400 pages. L. 4000. \$7.00

Besides other original papers, proceedings of "Symposia" are contained in :

Vol. 4° : On "Hybrid corn in Italy".

Vol. 5° : On "The agricultural problems of the Appenninic Mountains" and on "Recent wheat breeding in Italy".

Vol. 6° : On "Potato and Tomato breeding".

The last volume, the 7th, contains among others, the following papers :

"Defective caryopsis factors from maize-teosinte derivatives"—Spatial and pluriannual experiments in Agriculture. "A new method of placing inherited factors in maize?". A series of papers dealing with the Chinese agriculture written by the members of the Italian Agrobiological Delegation to China, (1956): General aspects of the Chinese Agriculture; Farm cooperation and economics; Exploitation of the "red grounds"; Industries connected with agriculture; Chinese pomology; Rice culture and rice breeding; Phytopathology and phytopathological control; College education and agricultural experimentation; Fishing and animal husbandry; Silkworms and genetics.

The 8th vol. is in press. Besides other original papers it contains the Proceedings of the 3rd annual meeting of the SIGA (Italian Society for Agricultural Genetics). The next volume, IX, will contain the proceedings of a Meeting on Lucerne and of the 4th annual meeting of SIGA.

*Orders may be sent to the editor or placed through book-sellers*

*Managing Editor:*

**Prof. C. JUCCI, Centro di Genetica del C.N.R. Palazzo Botta-Pavia, Italy.**

## COMMONWEALTH BUREAU OF PLANT BREEDING AND GENETICS

### SCHOOL OF AGRICULTURE, CAMBRIDGE, ENGLAND

Information on all topics concerned with the improvement of economic plants and microorganisms, in particular the methods and achievements of crop breeding, field trials, new varieties and strains, genetics, cytology and applied statistics is given regularly in the journal.

## PLANT BREEDING ABSTRACTS

### COMPILED FROM WORLD LITERATURE

Each volume contains four to five thousand abstracts from articles and reports in thirty to forty different languages, also reviews of new books and notices of new journals.

Subscription rate : 70s. or \$ 9.80 per volume (including indexes)

*Order through booksellers or to*

### COMMONWEALTH AGRICULTURAL BUREAUX

**Central Sales Branch, Farnham Royal, Slough, England.**



# EUPHYTICA

## Netherlands Journal of Plant Breeding

Vol. 9 (1960) contains 362 pp., among others, original articles (in English) on: Progressive necrosis in wheat hybrids; Wheat breeding in Kenya; Rust-resistance in some induced mutations of the New Pusa wheats 797,798 and 709; Meeting of the Eucarpia maize section in 1960; Linkage studies in rice; Tetraploid soybeans; Selection in tetraploid green gram varieties; Selection of pulses in Surinam; Efficient production of triploids in sugar beet; Relationship between growth and yield in cocoa varieties; A proposed classification of screening methods for plant breeding programs; Chromosome numbers in potato cultivars hypersensitive to late blight; Some data on the resistance against the potato root-eelworm in *Solanum kurtzianum*; Interspecific hybridization between *Corchorus* species; Cytogenetics of the trispecific hybrid *Nicotiana tabacum* × *glutinosa* × *trigonophylla*.

Published three times a year, in annual volumes of ± 300 pages. Annual subscription: 15 guilders (or 4 dollars). Vol. 10 appears in 1961. Vols. 1 (1952)—9 (1960) are still available at \$4 per volume.

Address all communications to : Dr. H. de Haan, Nude 66, Wageningen, The Netherlands.

## Journal of the INDIAN BOTANICAL SOCIETY

*The J. Indian bot. Soc. is a QUARTERLY now running Volume 39 (1960)*  
*The Annual Subscription is Rs. 30·00 or £ 2-10-0 or \$ 7·50 for a complete volume of four numbers.*

**BACK NUMBERS of the Journal and the following  
SPECIAL PUBLICATIONS of the Society are available:—**

- The Flora of Indus Delta—  
Rs. 5·50
- Professor M. O. P. Iyengar Com-  
memoration Volume—Rs. 30·00

### HISTORY OF BOTANICAL RESEARCHES IN INDIA, BURMA & CEYLON:—

- Part I—Mycology & Plant Pa-  
thology by Prof. S.N. Das Gupta  
Rs. 5·50
- Part II—Systematic Botany of  
Angiosperms by Rev. Fr. H.  
Santapau, S. J.— Rs. 4·70
- Part III—Paleobotany by Dr. A.  
R. Rao— Rs. 4·50
- Memoir I of the Society—  
Rs. 8·50
- Memoir 2 of the Society—  
Rs. 7·50

Further Particulars from:

The Business Manager & Treasurer,  
Indian Botanical Society,  
University Botany Laboratory,  
MADRAS-5, India.

## **IMPORTANT I.C.A.R. PUBLICATIONS**

### **FARMERS OF INDIA**

**Vol. I—Punjab, Himachal Pradesh and Jammu & Kashmir**

by

**DR. M. S. RANDHAWA and PREM NATH**

This is the first of a series of books on farmers of India which the Council is bringing out to promote proper understanding and appreciation of the problems of the farmers of the country so essential in formulating development plans and their successful implementation.

This volume gives a vivid portrayal of farmers of Punjab, Himachal Pradesh and Jammu & Kashmir. The climate, topography, soil, vegetation, crops and agricultural practices are described in detail. The book also tells us about the farming communities, their villages, homes, culture, way of life, beliefs and traditions. The account is very realistic and shows a profound understanding of rural life as shaped by history, geography, climate and religion. The hundred and odd photographs which illustrate the book catch the beauty of the landscape and the mood of the people, making it an intensely human document.

Pp. 302, (6½"×9½") Illustrations 109, Price Rs. 14·00 (Postage Rs. 2·50)

### **PRESERVATION OF FRUITS AND VEGETABLES**

by

**GIRDHARI LAL, G. S. SIDDAPPA, and G. L. TANDON**

This book is the result of intensive study and research over long years by three senior officers of the Central Food Technological Research Institute, Mysore. It deals with all aspects of the subject. Both the technician as well as layman will be interested in this book.

Pp. 356, (6¼"×9½") Illustrated. Price Rs. 11·50 (Postage Rs. 2·00)

### **ZYGNEMACEAE**

by

**DR. M. S. RANDHAWA**

This monograph fulfils a long felt need for a standard book on the subject. It deals with the genera and species of the Zygnemaceae, their structure and methods of reproduction, the concept of their evolution and the systems of classifications.

Pp. 478, (7½"×10") Illustrations 521, Price Rs. 26·00 (Postage 3·00)

### **CYANOPHYTA**

by

**DR. T. V. DESIKACHARY**

This monograph on blue-green algae is devoted to a description of general morphology including limnological aspects, biology in salt and marine habitats, symbiotic and parasitic associations and taxonomy.

Pp. 686, (7½"×10") Plates 139, Price Rs. 37·00 (Postage Rs. 3·00)

*Copies available from*

**The Business Manager,**

**INDIAN COUNCIL OF AGRICULTURAL RESEARCH,**

**Dr. Rajendra Prasad Road, New Delhi.**



**JUST PUBLISHED !!**

## **RICE IN INDIA**

*by*

R. L. M. GHOSE, M. B. GHATGE and V. SUBRAMANYAM

This monograph on rice—the major cereal crop of India—deals at length with all aspects of rice cultivation in India. Written by specialists, it incorporates the latest scientific research on the crop and results achieved upto date.

Beginning with a historical background, Part I deals with the botany, climate, soils, irrigation, rice culture, diseases and pests of rice. This is followed by a review of research conducted in various branches of the subject and recommendations and suggestions on improved methods, seeds, fertilizers etc.

Part II deals exhaustively with the problems of marketing and Part III with the technology of rice processing, nutritive value of rice and rice diets.

482 pages,  $7\frac{1}{4}'' \times 9\frac{1}{2}''$  (1960): Price Rs. 12·00 (Postage Rs. 3·00)

## **BEAUTIFUL CLIMBERS OF INDIA**

*by*

DR. B. P. PAL, Director, I.A.R.I., New Delhi

This publication contains a vivid description of the various types of climbers grown in the country. Practical suggestions for their selection and cultivation are given in the book. Written in a simple style, this profusely illustrated volume will be welcomed by lovers of flora, gardeners, nurserymen, amateur horticulturists, town planners, botanists and others.

109 pages,  $5\frac{1}{2}'' \times 9\frac{1}{2}''$  (1960): 39 colour plates: Price Rs. 8·00 (Postage Rs. 1·50)

## **DRY FARMING IN INDIA (Second Edition)**

*by*

N. V. KANITKAR, S. S. SIRUR and D. H. GOKHALE

The first edition of this monograph written by N. V. Kanitkar brought upto date the research work done in Dry Farming in India upto 1940. The present edition, with a comprehensive supplement by S. S. Sirur and D. H. Gokhale, gives upto date information on important aspects of Dry Farming, like soils of the problem areas, the disposal of rain water, surface run-off and soil erosion in scarcity regions, soil moisture fluctuations and water requirements of millets, etc., together with recommendations regarding soil conservation and dry farming applicable to those regions. The monograph will prove very useful as reference and guide book for all those interested in this vital subject, whether scientific workers, extension agents or practical farmers.

486 pages,  $6\frac{1}{4}'' \times 9\frac{1}{2}''$  (1960) 8 illustrations: Price Rs. 21·00 (Postage Rs. 3·00)

## **INDIGENOUS AGRICULTURAL IMPLEMENTS OF INDIA (An All-India Survey)**

This All-India Survey of Indigenous Agricultural Implements provides an exhaustive account of the various implements used by the farmers of various parts of India.

The book also contains recommendations of the survey committee, their general statements on representative types of Ploughs, Harrows, Hoes, Seed Drills, Rollers, Planks, Levellers, Ridgers and Harvesting Implements. The book will prove an indispensable guide to every Agriculturist, Extension Worker, Research Worker, Research Station, Library and will be valuable as a text book to students of agriculture.

402 pages,  $6\frac{1}{4}'' \times 9\frac{1}{2}''$  (1960) 139 illustrations: Price Rs. 10·50 (Postage Rs. 2·00)

*Copies available from:*

**The Business Manager,  
Indian Council of Agricultural Research,  
Dr. Rajendra Prasad Road, New Delhi.**



## INFORMATION FOR CONTRIBUTORS

THE INDIAN JOURNAL OF GENETICS & PLANT BREEDING is a periodical for the publication of records of original research in the field of genetics and plant breeding, and of cytology, physiology and other cognate sciences of sufficient importance and of such a character as to be of primary interest to the geneticist and the plant breeder. It will also, from time to time, contain articles summarizing the existing state of knowledge in the various branches of genetics and plant breeding. Papers by authors who are not members of the Indian Society of Genetics & Plant Breeding will not be accepted except in the case of invitation articles. It will be issued in parts as material and finances permit, and a volume will consist of one or more such parts.

Manuscripts should be sent to the Editor. Clearness, brevity and conciseness are essential; in form, style, punctuation, spelling and use of italics, manuscripts should conform to the best usage in the leading journals published in India and abroad. Manuscripts should be typed on one side of the paper, double-spaced and thoroughly revised before submission as no editing or material changes in the proof stage will be permitted, unless the extra cost involved is paid for by the author. Numerical data and calculations should be very carefully checked.

Papers should not ordinarily contain more than 6,000 words and should conclude with a brief summary of the principal points and important conclusions.

The names of authors, preferably unaccompanied by their degrees, titles, etc. should be written on the next line after the title of the paper followed by the name and address of the institution where the work was done.

Each table should have a heading stating its contents clearly and concisely. Places at which tables are to be inserted, should be indicated.

Generic and specific names should be underlined and the first reference to the latter should be followed by the authority. The first reference to common names of plants, etc. should be followed by their scientific names in parentheses.

All references to literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "REFERENCES" at the end of the article. In the list care should be taken to give the titles in full, and to indicate accurately in Arabic numerals, the volume number, the first and last pages, and the date of each paper if published in a periodical, and the place and date of publication and the name of the publisher, of each independent publication. The names of authors should be arranged in alphabetical order, and the papers under each author's name in chronological order. Where more than one paper by the same author appears in a single year they should be distinguished by *a, b, c, . . . .*. Titles of periodicals should be abbreviated according to the *World List of Scientific Periodicals* (1952).

Only illustrations which are of good quality and which are essential to a clear understanding of the paper can be accepted. Each illustration must be specifically referred to in the text. Text-figures should be used in preference to plates (half-tones, coloured plates not being accepted unless they are paid for by the author). Text-figures should be numbered in Arabic numerals, in order of their reference. Photographs for publication should be the best obtainable, of glossy finish, unmounted and sent unfolded. They should be attached lightly to paper on which should be written the plate number, title of the article and a short identifying legend. Roman numerals should be used in numbering the plates and in referring to them in the text. Legends of plates should not be inserted in the text but should be placed at the end of the manuscript. Individual illustrations within a plate should be designated by Arabic numerals.

Authors will receive 25 reprints without covers free; additional copies may be purchased and should be ordered when the proofs are returned.

Papers forwarded to the Editor for publication are understood to be offered to THE INDIAN JOURNAL OF GENETICS & PLANT BREEDING exclusively. It is also understood that the authors have obtained the approval of the Head of their Department, Faculty or Institute in cases where such approval is necessary.

The responsibility for statements, whether of fact or opinion, rests entirely with the writers thereof.



# **SPECIAL SYMPOSIUM NUMBER OF THE INDIAN JOURNAL OF GENETICS & PLANT BREEDING**

—: o :—

Contains the papers presented at the Symposium on "Genetics and Plant Breeding in South Asia" held at New Delhi in January, 1957. Printed on superior art paper. 310 pages.

"This well-published report is very attractive and useful for plant breeders all over the world" .. .. *Euphytica.*

"The Indian Journal of Genetics & Plant Breeding is to be congratulated for producing this volume of high technical excellence. It contains a wealth of ideas and information not only indispensable to workers in these and associated fields, but also to advanced students of Botany and Agriculture in our Universities" .. *Current Science.*

*Copies can be had from :*

**The Treasurer,  
Indian Society of Genetics & Plant Breeding,  
Division of Botany,  
Indian Agricultural Research Institute,  
New Delhi-12.**

**Price Rs. 25/-**

Students can purchase this volume at a concessional price.